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UNITED STATES DEPARTMENT OF AGRICULTURE
BULLETIN No. 1121

Washington, D. C. PROFESSIONAL PAPER December, 1922

THE EFFECTS OF INBREEDING AND CROSSBREEDING ON GUINEA PIGS

III. CROSSES BETWEEN HIGHLY INBRED FAMILIES

By SEWALL WRIGHT
Senior Animal Husbandman in Animal Genetics
Animal Husbandry Division, Bureau of Animal Industry

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By SEWALL WRIGHT, *Senior Animal Husbandman in Animal Genetics, Animal Husbandry Division, Bureau of Animal Industry.*

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INTRODUCTION.

It has been shown in Part I of this series of papers[2] that continuous mating of brothers with sisters in a stock of guinea pigs has been accompanied by a decline in all of the elements of vigor which have been studied. These include the percentage born alive, the percentage raised to weaning (33 days), birth weight, rate of gain to weaning, adult weight, size of litter, and number of litters produced per year. Just how much of the decline in these respects was due to inbreeding and how much to environmental conditions was not wholly certain. It was shown, however, that the inbred stock had

[1] The two preceding parts of these studies have been published as Bulletin 1090, U. S. Department of Agriculture.

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come to be distinctly inferior to a control stock in each of these respects and also in resistance to tuberculosis. It was concluded from a consideration of the various lines of evidence that the inbreeding was in some way responsible for at least a part of the decline.

In Part II [2] a detailed study was made of the 23 separate inbred families. It was shown that marked hereditary differentiation had been brought out among them early in the course of the inbreeding and that the differences had increased later. There had been also an automatic differentiation and fixation of the more obvious characteristics, such as color, pattern, and tendency toward polydactylism and toward the production of particular types of monsters. It was found that the various elements of vigor and weakness had become fixed in almost every possible combination in the various families, there being no evidence for hereditary differences in general vigor.

The purpose of the present paper is to present the results of crosses between the inbred families.

THE INBRED FAMILIES.

Of the 17 inbred families still in existence in 1916, only 5 have been retained to the present. It seemed necessary to eliminate the others in order to make room for the crossbreeding experiments and to obtain sufficient numbers from these five. Families 2, 13, 32, 35, and 39 were the ones retained, partly because they occupied a large number of pens, and partly because of contrasting characteristics. Family 39, for example, had the least white in the coat, while Family 13 had the most. Family 32 had a peculiar intense golden agouti. Families 2 and 13 were at opposite extremes in weight and also contrasted in size of litter.

CROSSBREEDING EXPERIMENTS.

The control stock, Experiment B, has been maintained, as from the first, by matings between individuals less closely related than second cousins.

Since 1916 a large number of first crosses have been made between different families. These constitute Experiment C0. The young are crossbred but the parents are inbred.

Some of the progeny from Experiment C0 have been mated with others from a different cross, thus bringing together four inbred families. This is Experiment CC. Both parents and young are crossbred in this case.

Other animals from Experiment C0 have been mated brother with sister. This is Experiment C1. The parents are crossbred but the young are to some extent inbred.

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[2] U. S. Department of Agriculture Bulletin 1090.

This renewed inbreeding has been continued in a small second generation of brother-sister mating, Experiment C2, in which both parents and offspring are, to some extent at least, again inbred.

In Experiment CA, inbred females were mated with crossbred males derived from two other inbred families. Experiment AC is the reciprocal, crossbred females mated with unrelated inbred males. The progeny of these two experiments should have approximately the same heredity. Differences in the results must be attributed to the direct influence of the dam or sire.

The nature of these experiments is indicated in Table 1, in which the result of prolonged inbreeding is represented by 0, crossbreeding by 1, and the first and second generation of renewed brother-sister mating by ½. It will be shown later that these figures represent accurately the differences to be expected among the experiments.

TABLE 1.—*The breeding of the sire, dam, and young in the various experiments.*

Items.	B.	Inbred.	C0.	CA.	AC.	CC.	C1.	C2.
Heredity of sire	1	0	0	1	0	1	1	½
Heredity of dam	1	0	0	0	1	1	1	½
Heredity of young	1	0	1	1	1	1	½	½

Two selection experiments were begun in 1918 among the crossbreds derived from the inbred stock. In Experiment CG only animals which were exceptionally heavy at weaning at 33 days were used (average weight, males, 307.7 grams; females, 298.1 grams). These naturally came in the main from small litters (average 1.7). In Experiment CL only animals from large litters were mated (average 4.3). These were generally light in weight (average, males, 214.1 grams; females, 207.0 grams), and seemingly much less thrifty than those in CG. In both cases, animals were chosen from any crossbreeding experiment (except B) and in a few cases from among the inbreds. The experiments were discontinued after 1919. While not carried on long enough to be satisfactory as selection experiments, they are of interest as throwing light on the question as to how far any conscious or unconscious selection of young on the basis of vigor could account for the observed difference between experiments.

DESCRIPTION OF TABLES.

The results in the various experiments during the years 1916 to 1919 are shown in detail in Tables 14 to 21 and are summed up in Table 29.

Table 14 gives data on the fertility. The number of litters and the average size of litter are given for each experiment. The number of mating years was calculated as described in Part I.[3] Each mating

[3] U. S. Department of Agriculture, Bulletin 1090.

was entered as mature under the month in which the male reached 4 months of age or under the month following mating if he was already 3 or more months old. The mating was dropped in the month following the death or disposal of the female. The number of months of mating in the experiment, divided by 12, gives the number of mating years with sufficient accuracy for use in calculating the average number of litters per year, young per year, and young raised per year, which are given in the last three columns of Table 14.

Table 15 presents data on the percentage of the young born alive (or at least found alive) in each experiment during the years 1916–1919. The total percentage is given in the next to the last column. This is not necessarily the best measure of the relative standing of the experiments in success in bearing living young under fixed conditions, as has been discussed in Part I. The percentages are accordingly given separately for each size of litter and an index is given (last column) for the purpose of showing the standing of the experiments free from the influence of size of litter. In the present paper this index is derived by assigning weights of 1, 3, 3, and 1 to the records of litters of 1, 2, 3, and 4, respectively.

The desirability of using such an index may be seen by comparing the records of the first two inbred families (Nos. 2 and 13). Family 13 is superior to Family 2 in the percentage born alive in each size of litter except in litters of 4, yet in total percentage born alive it comes out markedly inferior. The explanation is merely that Family 13 produced a greater number of large litters. The index brings out better the true relation under constant conditions.

So far as the crossbreeding experiments are concerned, it makes very little difference whether the total percentage or the index is used. This is because size of litter has less effect on mortality of the young than among the inbreds.

There are, of course, other conditions which affect the percentage born alive, the uniformity of which must be considered before making a final interpretation of the results. The more important of these conditions will be taken up later after consideration of the other tables.

The data on the percentage raised to 33 days of the young born alive are presented in a similar way in Table 16. The index given in the last column is derived in the same way as described above. The product of these percentages, the percentage raised to 33 days of all young born, is treated in the same way in Table 17.

In the case of birth weight (Table 18) the effect of size of litter is so great that the actual average in an experiment means very little. The average birth weight in one of the inbred families (No. 35), for example, is greater than that in Experiment AC (72.6 compared with 72.1). This, however, is not as significant as the fact

that AC is markedly superior in the average for any given size of litter. The latter fact is brought out in the index, obtained as in the cases of the mortality percentages, by assigning weights of 1, 3, 3, and 1 to litters of 1, 2, 3, and 4, respectively.

The differences among the experiments in the percentage of the young which die before weaning have an effect on their standing in average birth weight, since such young are in general below the average. The average birth weight of the young which reach 33 days (Table 19) thus gives a better measure of the normal prenatal growth rate and also is needed in calculating the rate of gain between birth and weaning.

The averages and indices for weight at weaning (33 days) are dealt with in Table 21. The rate of gain between birth and weaning, obtained from the data in Tables 19 and 21, is given in Table 20.

ALLOWANCE FOR SEASONAL FLUCTUATIONS.

Size of litter is of course not the only factor for which allowance must be made in studying the effects of breeding on the various characters. The most important factor is undoubtedly the environmental situation. It would be highly desirable to compare the records only in experiments which were conducted simultaneously and under the same conditions. There are, however, practical difficulties in carrying through such a project. Some of the present experiments were carried on through the whole four years 1916–1919, but others were started or dropped at intermediate times. Table 22 shows the average number of mature matings in each experiment during each 3-month period, beginning with January to March, 1916, and ending October to December, 1919. The number of litters, the number of young, the number of young born alive, and the number raised in each experiment during each of these periods are shown in Tables 23 to 26.

The environmental conditions were unfortunately exceptionally varied during the four years which we are considering. There were three times—the winters of 1915–16 and 1916–17 and the spring of 1918—when the stock did very poorly, due partly to unusual winter conditions, extreme variations in temperature, poor ventilation, etc., but probably in the main to insufficient green feed. In all of these periods symptoms, such as lameness and bleeding at the gums, appeared, which were probably indications of scurvy. There have been no real epidemics of contagious disease, although many old animals died in the periods noted above. The stock reached fairly good condition during each fall; and good condition was maintained through all of 1919.

The records of the total inbred stock have been tabulated for each 3-month period during 1916 to 1919. A summary of the indices and

averages is given in Table 27. The results are presented graphically in Figures 1 to 7. The periods of depression and of good condition are clearly brought out. In a general way there is agreement between the fluctuation of the percentage born alive, the percentage raised of those born alive, birth weight, rate of gain, and size and frequency of litters. Figure 6, which shows the number of young raised per year by the average mating in each period, perhaps reveals best the changes in environmental conditions. The probable absence of relation between sex ratio and season may be seen by comparing Figure 7 with Figure 6.

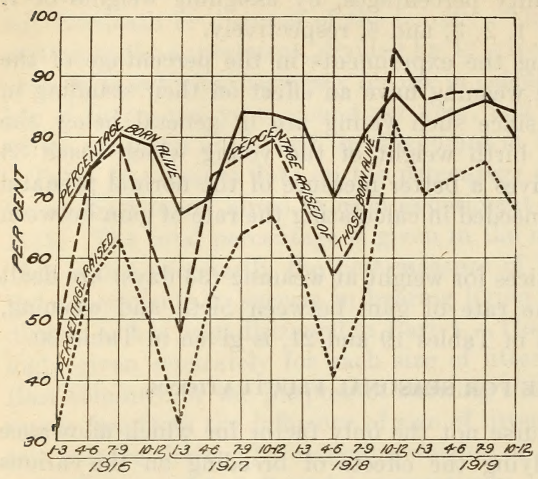

FIG. 1.—The percentages born alive, raised of those born alive, and raised of all young, in the inbred stock during successive 3-month periods, 1916–1919.

There are various ways in which allowance could be made for these fluctuations. The method which has been adopted is to compare the actual average or index for each experiment for the entire period in which it was maintained with the estimated record of the total inbred stock produced simultaneously. As an example, we see in Table 22 that there were 0.3 mature matings in Experiment C1 in the period July–September, 1916. The record of the inbreds as regards frequency of litter during this period is given in Table 27 as 3.35. Multiply these together and add the similar products for subsequent periods in the history of C1. On dividing by the total number of mature matings (3 months'

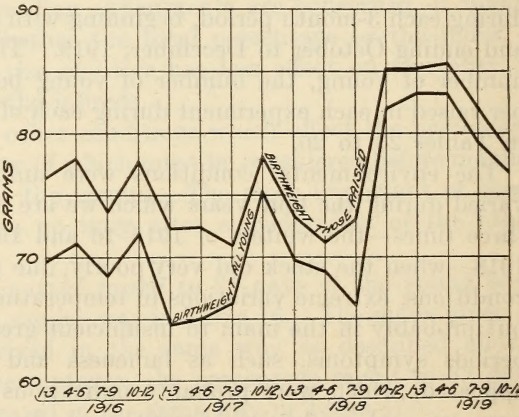

FIG. 2.—The average birth weight of young raised to weaning (33 days) and of all young born in the inbred stock during successive 3-month periods, 1916–1919.

duration) we obtain the desired estimate for inbreds producing litters simultaneously with Experiment C1.

In dealing with other characteristics, the number of matings present in each 3-month period does not necessarily provide the proper weights to be applied to the records of the inbreds. Litters per year, young per year, and young raised per year are properly weighted by the number of matings, but in the case of size of litter the number of litters produced by the given experiment in each 3-month period (Table 23) should be used. The percentage of young born alive, the percentage raised of all born, and the birth weight of all born should be weighted by the number of young born in each 3-month period as given in Table 24. There is a slight impropriety here, owing to the use of indices for these characters, but it is of no practical importance. Similarly the percentage raised of the young born alive is to be weighted by the numbers born alive, shown in Table 25. The birth weight of the young raised, the rate of gain to weaning, and the weight at weaning are to be weighted by the numbers weaned in each period, shown in Table 26. The estimated record of the inbreds, simultaneous with each experiment, is shown for each character in Table 28.

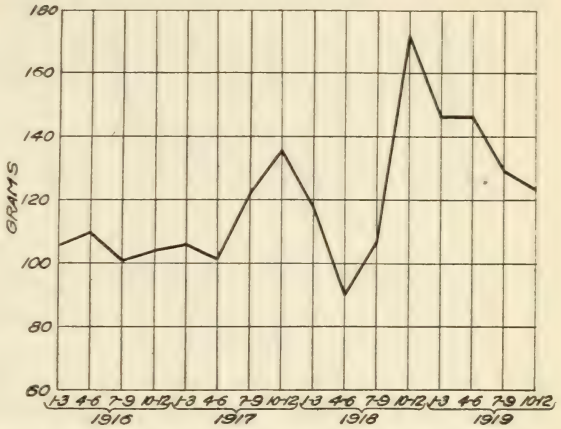

FIG. 3.—The average gain between birth and weaning (33 days) in the inbred stock during successive 3-month periods, 1916–1919.

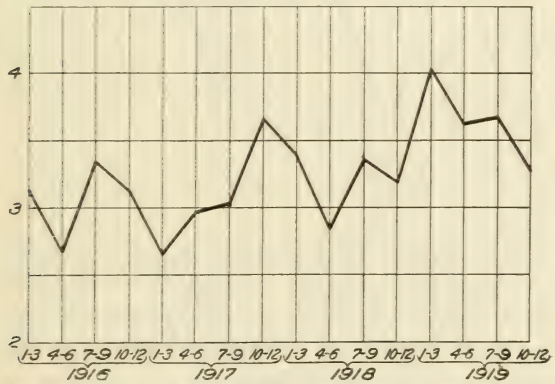

FIG. 4.—The average number of litters produced per year by mature matings in the inbred stock during successive 3-month periods, 1916–1919.

This method of correcting for the seasonal fluctuations rests on the assumption that the condition of the total inbreds was genetically constant during the four years. Theoretically one would expect practical constancy in each family after a dozen generations of brother-sister mat

ing. The records in four previous years, 1911–1915, as well as in these years show that the total inbred stock rose and fell in close parallelism with the control stock. The rising records for the years 1916–1919 certainly give no evidence of continued genetic decline. It would have been desirable to have used only one family as a criterion of the rise and fall in environmental conditions if sufficient numbers had been available. As it was, it seemed best to use the total inbred stock. This stock was largely composed of five families which were kept up to about the same proportional representation during this period. The combined averages for the other families, moreover, were close in most respects to the average of these five important families.

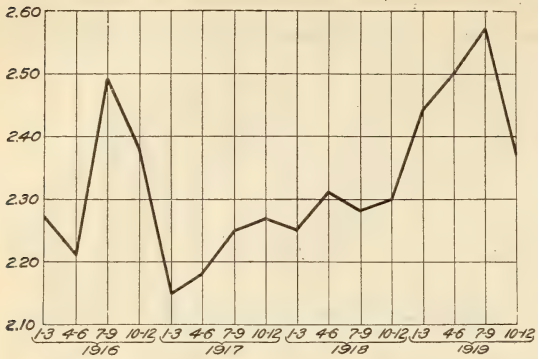

FIG. 5.—The average size of litters produced by the inbred stock in successive 3-month periods, 1916–1919.

A comparison of the entries in Table 28 with the corresponding ones in Table 29 brings out, it is believed, the superiority or inferiority of each experiment to the total inbred stock, free from the influence of seasonal fluctuations and of size of litter on the other characters.

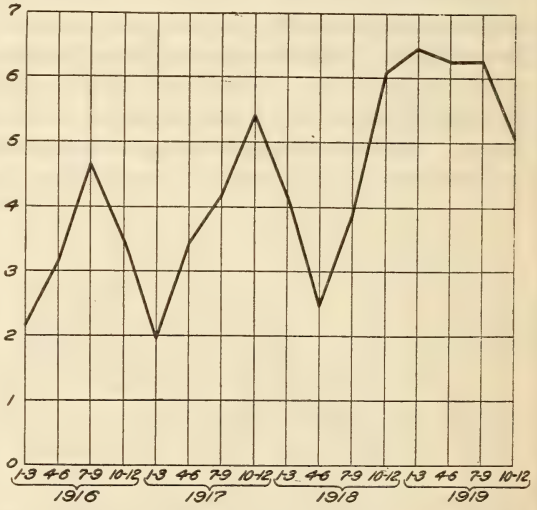

FIG. 6.—The average number of young raised per year, by mature matings, inbred stock, during successive 3-month periods, 1916–1919.

TABLE 2.—*The superiority (+) or inferiority (−) of the record of each experiment to that made by the inbred stock at the same time.*

[With respect to the first three characteristics (percentage born alive, percentage raised of those born alive, and percentage raised) the difference from the record of the inbred stock is corrected as described in the text. With respect to the other characteristics, the differences are given as percentages of the record of the inbred stock.]

Experiment.	Percent born alive.	Percent raised of those born alive.	Percent raised.	Birth weight, total.	Birth weight, those raised.	Gain.	Weight at 33 days.	Size of litter.	Litters per year.	Young per year.	Young raised per year.
2	−3.8	+3.3	−0.3	−9.4	−7.7	−18.6	−14.4	−3.6	+12.9	+8.8	+13.1
13	−1.4	−1.5	−2.8	+3.4	+6.1	+13.2	+10.4	+7.8	0	+7.8	+2.1
32	+2.3	−6.0	−2.3	+2.3	+0.8	+0.3	+0.4	−6.5	+1.5	−5.1	−7.8
35	+0.7	+4.3	+3.3	+5.8	+4.6	+11.8	+9.0	+4.2	+9.7	+14.3	+16.1
39	+4.3	−5.3	−0.4	−4.6	−5.2	−1.1	−2.6	+1.0	−8.4	−7.5	−11.9
Other	+1.0	−1.6	−1.6	+2.8	+1.6	+0.6	+1.0	−1.6	−11.9	−13.3	−15.2
CO	+0.5	+11.2	+9.2	+1.7	+2.5	+13.2	+9.0	−1.8	+0.8	−1.0	+9.5
CA	+2.7	+12.4	+10.4	+3.6	+3.6	+11.7	+8.6	+3.6	+19.4	+23.6	+47.4
AC	+7.6	+11.8	+14.7	+8.8	+8.1	+11.9	+10.5	+28.3	+9.3	+40.2	+63.7
CC	−6.9	+12.0	+14.6	+12.9	+9.2	+21.0	+16.5	+14.3	+36.1	+55.4	+82.5
C1	+9.0	+9.3	+13.9	+10.7	+7.1	+15.9	+12.5	+10.2	+33.3	+46.9	+73.1
C2	+3.8	+7.9	+8.9	+6.7	+4.5	+12.7	+9.8	+4.0	+25.0	+29.9	+43.7
CL	+9.8	+4.8	+11.5	+8.3	+4.5	+21.7	+15.3	+14.2	+17.8	+34.5	+56.2
CG	+5.1	+5.9	+8.8	+8.0	+8.4	+19.5	+15.3	+15.1	+27.0	+46.1	+53.4
B	−8.6	+10.8	−14.9	+10.8	+9.4	+18.9	+15.2	+14.0	+14.1	+30.1	+60.2

The actual differences are shown in Table 30. In Table 2 the differences in the case of the weights and fertility are shown as percentages of the record of the total inbred stock. Experiment B, for example, produced litters 14 per cent larger than the inbreds. In the case of the mortality data, the actual differences shown in Table 29 are modified to allow for the influence of different basic percentages in the inbred stock. To illustrate, 69.4 per cent was the percentage of the inbreds raised to 33 days while Experiment AC was in progress. Only 58.9 per cent were being raised simultaneously with CC. There is more room for improvement in the latter case. Thus the 8.2 per cent advance of AC beyond the inbreds may mean as much as the advance of 11.9 per cent shown by CC. A correction has been applied according to the method described in a previous paper (Wright, 1920)[4] in connection with the percentage of white in the coats of guinea pigs. Assume that the distribution of the animals in a given stock relative to conditions which make for survival or death follows approximately a normal probability curve. The area to one side of a certain ordi-

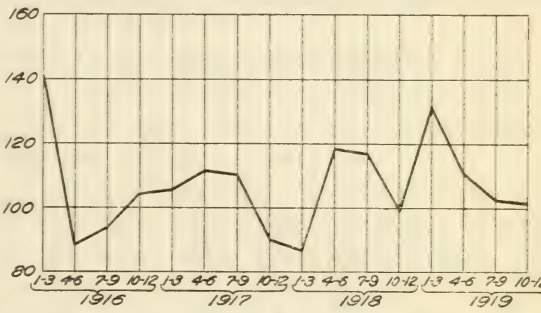

FIG. 7.—The sex ratio (number of males per 100 females) among the young born in the inbred stock during successive 3-month periods, 1916–1919.

[4] See "Literature cited" at end of bulletin.

nate represents the percentage of deaths, to the other side, survivals. The change in the percentage of deaths due to a given shift in the conditions is equal to the area between two ordinates at a given distance apart. This area is of course greater at the middle of the curve (50 per cent deaths) than toward either limit. On this hypothesis a table of probability integrals can be used for comparing percentage differences at different points of the range between 0 per cent and 100 per cent.

The numbers in Table 2 give the departure of each experiment from the total inbred stock, adjusted on the above basis to the record of the latter for the whole four years 1916–1919, i. e., 77.7 per cent born alive, 72.1 per cent raised of those born alive, and 56.3 per cent raised. This correction, it will be noticed, makes the records of AC and CC, with which this discussion started, approximately equal. So far as most of the conclusions are concerned, it makes little difference whether the correction is made or not. It seems important, however, to show the order of effect.

ALLOWANCE FOR HEREDITY.

Another consideration, which has doubtless occurred to the reader in comparing the records of the inbreds and crossbreds, is the exact heredity of the latter. There are fairly large differences among the inbred families themselves. If only animals from the better families were used in making crosses, the latter would naturally be superior, apart from the effect of the system of mating.

TABLE 3.—*The inbred ancestry of the males and females used in the various crossbreeding experiments, in percentages.*

[Each mating weighted by the number of litters produced through 1919.]

Inbred family.	C0.		C1.	C2.	CC.		CA.		AC.	
	Sire.	Dam.			Sire.	Dam.	Sire.	Dam.	Sire.	Dam.
2	16.1	19.3	9.7	8.0	5.4	5.8	20.9	18.4	16.9	27.0
13	7.7	23.6	16.1	8.0	16.3	23.7	21.8	42.4	18.0	15.2
32	5.3	7.2	4.2	5.3	5.6	2.9	8.5	26.6	15.7	7.0
35	11.1	5.1	6.5	0	7.5	4.2	9.8	12.0	27.3	7.0
39	16.6	7.9	18.3	18.7	21.0	17.7	17.7	0.6	17.4	17.3
7	4.8	2.7	0.6	0	1.0	2.5	0	0	0	3.2
9	3.1	3.8	4.7	5.3	0	1.0	0.9	0	0	2.0
17	3.8	6.8	8.7	12.0	6.5	1.0	1.3	0	3.5	0.6
18	4.1	1.2	3.0	0	0.6	2.5	1.3	0	0	2.9
20	4.1	6.5	3.6	8.0	3.5	5.8	2.5	0	0	5.3
23	7.0	2.1	2.4	0	7.9	4.2	2.5	0	0	1.7
24	0	0.9	0	0	0	0	1.3	0	0	0
31	4.6	2.7	4.4	10.7	4.0	5.0	1.6	0	0	1.7
34	3.8	1.7	2.8	0.7	10.5	7.9	9.5	0	0	1.2
36	5.5	4.1	6.7	8.0	5.4	4.0	0	0	0	4.7
38	2.4	4.4	8.3	15.3	4.8	11.8	0.3	0	1.2	3.2
OI	43.2	36.9	45.2	60.0	44.2	45.7	21.3	0	4.7	26.5

As it was, however, an effort was made to use all of the families. So far as any preference was given it was to the weaker ones. The inbred ancestry of the sires and dams of the litters produced in each

crossbreeding experiment is shown in Table 3 by percentages. These percentages can be applied to the differences between each inbred family and the total inbred stock as shown in Table 2 in order to find the extent to which the ancestry of the various crossbreeding experiments was above or below the average.

TABLE 4.—*The estimated superiority (+) or inferiority (−) of the inbred ancestors of the crossbreds to the total inbred stock.*

[The figures are based on the percentages given in Table 2 and may be compared with the actual superiority of the crossbreds over the inbreds as shown in that table.]

Experiment.	Per cent born alive.	Pern cent of those born alive.	Per cent raised.	Birth weight (total).	Birth weight of those raised.	Gain.	Weight at 33 days.	Size of litter.	Litters per year.	Young per year.	Young raised per year.
C0:											
Sire	+0.6	−1.0	−0.8	0.0	−0.4	−0.6	−0.5	−0.4	−3.3	−3.7	− 4.9
Dam	−0.2	−0.9	−1.3	+0.1	+0.4	+0.3	+0.3	+0.4	−2.0	−1.6	− 3.3
CA:											
Sire	+0.1	−1.0	−1.0	−0.7	−0.3	+0.1	−0.1	+0.6	−0.3	+0.3	− 1.2
Dam	−0.6	−1.1	−1.5	+1.0	+1.9	+3.7	+2.9	+1.4	+3.9	+5.2	+ 3.1
AC:											
Sire	+0.4	−0.5	−0.2	+0.3	+0.4	+2.3	+1.5	+1.0	+3.0	+4.1	+ 3.0
Dam	0.0	−0.8	−0.9	−1.5	−1.2	−2.2	−1.8	−0.2	−0.3	−0.6	− 1.6
CC:											
Sire	+1.1	−1.9	−1.2	+0.9	+0.6	+2.1	+1.5	+0.5	−5.5	−4.9	− 7.4
Dam	+0.8	−1.8	−1.4	+1.0	+1.0	+2.6	+2.0	+1.1	−5.7	−4.6	− 7.4
C1	+0.8	−1.6	−1.2	+0.5	+0.3	+1.2	+0.9	+0.4	−5.0	−4.6	− 6.7
C2	+1.1	−2.1	−1.4	+0.5	−0.1	−0.3	−0.2	−0.8	−7.6	−8.3	−10.5

The results are shown in Table 4. It will be seen that while the ancestors of the crossbreds were slightly above the average in some respects, as in weight and percentage born alive, in other respects they were below the average, notably in frequency of litter and the characteristics which depend on it.

In all important cases the corrections which might be made are small compared with the actual differences among the experiments. It is clear that these differences are not due to selection of superior inbred families in making the crosses.

In the case of the selection experiments CG and CL, the most important consideration relative to ancestry is the degree to which they were derived from different crossbreeding experiments. This is shown in Table 5.

TABLE 5.—*The origin of the males and females used in experiments CL and CG, in percentages.*

[Each mating weighted by the number of litters produced through 1919.]

Experiment.	CL.		CG.		Experiment.	CL.		CG.	
	Sire.	Dam.	Sire.	Dam.		Sire.	Dam.	Sire.	Dam.
Inbred	5.2	4.5	0	1.0	AC	12.7	16.4	1.5	11.4
C2	9.0	0	3.0	9.4	CC	15.7	16.4	18.8	12.9
C1	33.6	32.1	5.9	20.8	CL	17.9	18.7	0	0
C0	3.7	11.9	26.7	21.8	CG	0	0	36.1	22.8
CA	2.2	0	7.9	0					

ALLOWANCE FOR AGE OF DAM.

Another conceivable cause of differences among the experiments is the percentage of litters produced by immature females. The percentage of first litters in each experiment is shown in Table 6.

TABLE 6.—*The first litters from immature parents (mated at one or two months of age) as percentages of the total number of litters (1916–1919).*

Experiment.	Per cent.	Experiment.	Per cent.	Experiment.	Per cent.	Experiment.	Per cent.
2	14.3	39	15.3	CO	21.6	C1	20.5
13	18.8	Other	16.2	CA	23.8	C2	25.3
32	18.4	Inbred	17.4	AC	20.1	CL	25.4
35	22.3	B	8.3	CC	16.8	CG	23.8

Assuming that first litters are at a disadvantage, Experiment B should be superior to the inbreds, Experiment CC should be practically the same, while the other crossbreeding experiments should be inferior. However, as pointed out in Part I, the slight inferiority of first litters found in the present stock of guinea pigs is almost wholly a seasonal complication. A majority of the matings have been made in summer and fall under favorable conditions, bringing a majority of the first litters in winter and spring, when conditions are apt to be poor. It is found that on making proper correction for season, the low records for first litters born when the female is about 6 months old, as well as the similarly low records near 18 months of age, are brought almost to the 12-month and 24-month levels. It may safely be asserted that the differences in the average age of the dams in the various experiments are negligible as causes of differences in their records.

ALLOWANCE FOR SEX.

There is a slight difference between the birth weight of males and females and a slightly greater difference in their weaning weights. Since, however, the sex ratio (Table 7) in no case departs widely from equality, it has not been deemed necessary to find separate averages for the sexes.

TABLE 7.—*Sex of young born in each experiment, 1916–1919.*

[Those of unknown sex were in general found dead and in bad condition.]

Experiment.	Males.	Females.	Sex unknown.	Total.	Males per 100 females.	Experiment.	Males.	Females.	Sex unknown.	Total.	Males per 100 females.
2	514	444	40	998	115.8	CC	297	303	17	617	98.0
13	350	361	29	740	97.0	C1	302	317	10	629	95.3
32	237	245	6	488	96.7	C2	94	87	1	182	108.0
35	429	398	6	833	107.8						
39	195	177	10	382	110.2	CL	183	186	12	381	98.4
						CG	285	277	19	581	102.9
Other	564	567	39	1,170	99.5						
Inbred	2,289	2,192	130	4,611	104.4	B	761	762	36	1,559	99.9
CO	653	647	34	1,334	100.9						
CA	206	202	2	410	102.0	Total	5,341	5,262	272	10,875	101.5
AC	271	289	11	571	93.8						

There are certain interrelations among the characters, such as between percentage born alive and percentage of those raised, and between frequency and size of litter, of which account will be taken later in interpreting the results.

SIGNIFICANCE OF DIFFERENCES.

The records of the various experiments have now been corrected for the effects of size of litter and seasonal conditions, and it has been shown that no other important corrections need be made. It remains to be shown that the resulting differences (Table 30) are statistically significant.

The general significance of the differentiation among the inbred families has already been shown (Part II, Bulletin 1090) through the existence of high correlations between the records of the families in 1916–1919, and their records in 1911–1915 and 1906–1910. The considerably greater differences among the experiments relative to the system of mating fall into a consistent scheme which of itself leaves little doubt as to the general significance.

As to particular cases, the probable error of size of litter has been calculated by the usual formula, $PE = .6745 \frac{\sigma}{\sqrt{n}}$ where σ is the standard deviation, which may be calculated from the data in Table 14 and n is the number of litters.

The same type of formula has been used in the cases of litters per year, young per year, and young raised per year. If n is the number of mating years, σ is the standard deviation of number of litters, number of young, or number of young raised, respectively, during a year. An estimate of these standard deviations was made by tabulating the records for the first year after maturity for all matings which lasted at least 12 months. The records for the second and third full years were also used where available. The means and standard deviations were calculated for each group (Families 2, 13, etc., Experiments CO, CA, AC, etc.). As the standard deviations of these individual groups were rather irregular, owing to small numbers, it seemed best to use the average standard deviations in calculating the probable errors, making allowance for the correlation between mean and standard deviation, a correlation which is very important in the case of litters per year. Combining all of the above data, there was an average of 3.77 litters per year, 9.27 young per year, and 6.56 young raised per year. Letting X, X', and X'' represent the departures from these averages in any particular case, the standard deviations can be fitted reasonably well by the formulæ, $0.93 - 0.50X$ for litters per year, $3.19 + .13X'$ for young per year, and $2.57 + .05X''$ for young raised per year. The probable errors in Table 31 were calculated from the formulæ $PE = 0.6745 \frac{\sigma}{\sqrt{n}}$ where n is the number

of mating years (Table 14) and σ is calculated from the above formulæ, using the means in Table 14.

The formula for the probable error of a percentage (p) is $0.6745\sqrt{\frac{p\,(1-p)}{n}}$. In applying this to percentage born alive, the question arises as to whether n should be the number of individuals (in litters of 1 to 4) or the number of litters. In the former case $\sqrt{n}$ is about 50 per cent larger than in the latter. A compromise is in line with the system of indices which has been used. Accordingly, n has been taken as the number of individuals born in litters of 1 to 4, but the resulting estimate of the probable error has been increased by 25 per cent, i. e., $PE=1.25\times0.6745\sqrt{\frac{p\,(1-p)}{n}}$.

The percentage raised of the young born alive has been dealt with similarly, n being the number born alive in litters of 1 to 4. In the case of the percentage raised of all young, n is again the total number born in such litters.

Similar considerations apply in the case of the weights. The formula $PE=1.25\times0.6745\frac{\sigma}{\sqrt{n}}$ has been used in each case, n being the total number born in litters of 1 to 4 in the case of the birth weight of all young, and merely the number raised in such litters in the other cases. The standard deviations for a given size of litter have been taken as 14.76 grams for birth weight of all young, 13.62 grams for birth weight of young raised, 1.285 grams per day for gain, and 49.53 grams for 33 days' weight. These figures apply to litter means and follow from the following determinations based on an analysis of 3,009 litters of inbreds and controls:

Birth weight (total) ..... $\sigma_B' = 19.49$ grams.
$r_{BL} = -0.6580 \pm 0.066$.
${}_L\sigma_B' = 14.76$ grams.

Birth weight (raised) ..... $\sigma_B = 18.09$ grams.
$r_{BL} = -0.6580 \pm 0.066$.
${}_L\sigma_B = 13.62$ grams.

Gain ..... $\sigma_G = 45.87$ grams (33 days).
$r_{GL} = -0.3807 \pm 0.0105$.
${}_L\sigma_G = 42.42$ grams $= 1.285$ grams per day.

Weight at 33 days ..... $\sigma_{33} = 57.58$ grams.
$r_{BG} = +0.5326$.
${}_L\sigma_{33} = 49.53$ grams.

The formula for standard deviation for a given size of litter (L) is of the type

$$ {}_L\sigma_B = \sigma_B\sqrt{1-r^2_{BL}}. $$

The formula for ${}_L\sigma_{33}$ is derived from the equation

$$ {}_L\sigma_{33}{}^2 = {}_L\sigma_B{}^2 + {}_L\sigma^2{}_G + 2{}_L\sigma_B \cdot {}_L\sigma_G \cdot {}_Lr_{BG}. $$

The probable errors derived from these formulæ are given in Table 31 for comparison with the values shown in Table 29, and the differences between experiments shown in Table 30. The probable errors of the differences are from 10 to 20 per cent larger than the figures shown.

Before closing the discussion of probable errors there is one other point which should be brought up. We have based the probable errors on the number of litters or on a compromise between number of litters and number of individuals designed to allow for the correlation between litter mates. But the characteristics with which we are dealing here are wholly or in part characteristics of the parents. Should we not therefore base the probable errors on the number of matings? We have, however, previously (Part I, Bulletin 1090) called attention to the fact that there is no significant correlation between the successive records of a given mating as to size of litter, interval between litters, birth weight, and gain (Experiment B). This can also safely be affirmed of the mortality among the young. Thus persistent good or poor health of the dam or sire can be of very little importance in determining these characters.

In most experiments the parents are either inbreds or first crosses between inbred families and thus should be homogeneous genetically. In these cases there would seem no question that the litter, if not the individual, is the proper unit in calculating probable errors of experiment averages. In the cases in which segregation should be taking place among the parents (C2, CL, CG, and B) the propriety of this course depends on the number of factors involved. If only one allelomorphic series of factors were involved in the differences among the families in a given respect, the testing of only a few second generation females in C2 might give very misleading results, whatever, the number of litters produced by each one. If, however, many factors are involved, as is probably the case, the genetic heterogeneity should be less. It is believed that a sufficient number of matings was made in all cases to make the parents a fair sample of their respective experiments. The number of matings which produced young is given for each experiment in Table 10.

RESULTS.

We have concluded that the differences between each experiment and the inbreds as shown in Table 2 give a satisfactory basis for comparison.

The same results are shown graphically in Figures 8 to 19. A general survey of the figures establishes beyond question that marked improvement in every respect is brought about by crossbreeding. The characters, however, fall into two rather sharply opposed categories. In some of them there is little or no improvement in the

first cross, though marked improvement in the next generation. The percentage born alive, birth weight, size of litter, and frequency of litters come here. In the cases of percentage raised of those born alive, and gain, there is on the other hand marked improvement in the first cross.

THE PERCENTAGE BORN ALIVE.

A number of points of interest are brought out in Figure 8 in reference to the mortality at birth. It is shown that there is considerable variation among the inbred families, but that no one of them has as good a record as the random-bred stock (B). There is only a slight improvement, too small to be relied upon, when two families are

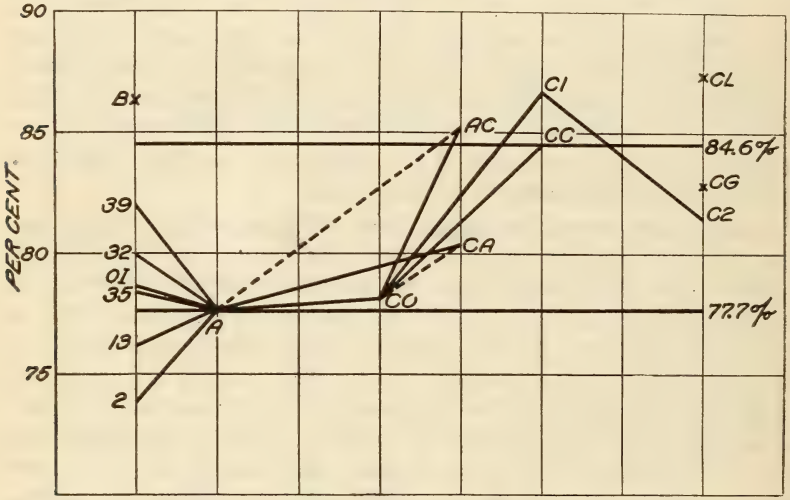

FIG. 8.—The percentage born alive, 1916–1919. Indices correcting for effects of size of litter and seasonal conditions: 2, 13, 32, 35, 39, inbred families; 0I, other inbred families; A, average of all inbreds; C0, first cross between inbred families; CA, crossbred male from C0, unrelated inbred female; AC, inbred male, unrelated crossbred female from C0; CC, crossbred male, unrelated crossbred female; C1, crossbred brother and sister from C0; C2, brother and sister from C1; CL, selection for large litters, small weight; CG, selection for small litters, large weight; B, random-bred stock.

crossed (C0). When, however, the crossbred females produce young, whether mated with an unrelated crossbred (CC), with a brother (C1), or with an unrelated inbred (AC), there is a substantial improvement which goes beyond the best of the inbred families and reaches practically the level of the random-bred stock. In contrast with the good record of Experiment AC is the relatively small improvement over the inbreds in the reciprocal cross CA, in which inbred females are mated with unrelated crossbred males. It is clear from these results that crossbreeding increases the number of young born alive, but that the breeding of the dam, not that of the young themselves, is the critical factor. The most significant line of cleavage between high and low records falls between Experiments A, C0, and

CA, in which inbred females are mated in various ways, and Experiments CC, C1, and AC, in which the females are crossbred. *A priori*, one might expect that the inherent vigor of the young would count for something, and the slight improvement in Experiments C0 and CA can be interpreted in this way. The superiority of C1 to CC, however, does not support this view. These experiments differ only in that the young of C1 are to some extent inbred. The superiority of CA over C0 might be interpreted as due to a direct influence of the vigor of the sire, but the similar superiority of AC over CC is opposed. All of these minor differences may, of course, be due to chance.

Turning to the other experiments, we find that C2 is intermediate between the group with inbred dams and the group with crossbred dams. This is to be expected, since in C2 the dams as well as the young are inbred, though not as much as the dams in A, C0, and CA. Theoretically, as will be brought out later, C2 should be just halfway between the inbreds and Experiment CC.

Experiments CL and CG have averages close to the other crossbreeding experiments. The superiority of CL over CG seems to be due merely to chance. Recalling that the mated animals in CG were exceptionally vigorous when weaned, while those in CL were only two-thirds as heavy and usually unthrifty in appearance, it must be concluded that the females completely recover from setbacks early in life as far as ability to bear young successfully is concerned. It may also be concluded that the superiority of Experiments AC, CC, and C1 over the inbreds is not due in the slightest to unconscious selection of relatively more thrifty animals in making the matings.

In this discussion we have been considering the indices, in which there is correction for the effect of size of litter. In Figure 20 Experiments C0, CC, C1, B, and the inbreds are compared, taking each size of litter separately. These experiments were in progress practically at the same time, so that it is not necessary to make a correction for seasonal effects. The inferiority of the inbred females (inbreds, C0) is clearly brought out. It also appears that this inferiority is most marked in the larger litters. Large litters are at only a slight disadvantage as compared with small ones in the case of crossbred dams, but have a markedly higher death rate than small litters in the case of inbred dams.

Summing up, the fate of the young at birth depends primarily on the breeding of the dam, as far as it is genetic at all. Crossbred females mated in any way are able to produce a distinctly larger percentage of living young than females of the best of the inbred families which entered into their composition. The inferiority of inbred females is greatest in large litters. About half of the superiority of the crossbreds is lost in the progeny of females from the first

generation of renewed inbreeding. The apparent thriftiness of the females in their early life gives no clue to their later success in bearing young.

THE PERCENTAGE RAISED AMONG THE YOUNG BORN ALIVE.

On comparing Figure 9 with Figure 8, which we have just been considering, the difference in the positions of Experiments C0 and CA at once attracts attention. In fact, as regards the percentage raised of the young born alive, every crossbreeding experiment is above the average of the best inbred families. It is clear that the breeding of the young is an important factor in the mortality between birth and weaning. The relatively advanced stage of development at which guinea pigs are born and their ability to care for themselves at a very

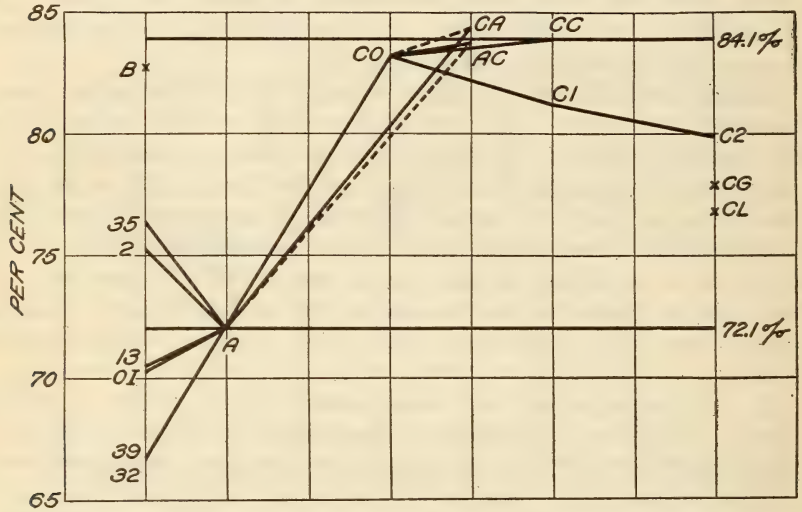

FIG. 9.—The percentage raised of the young born alive, 1916–1919. Indices correcting for effects of size of litter and seasonal condition. (See Fig. 8 for explanation of symbols.)

early age come to mind here. Experiment C0 is like the inbreeding experiments as regards breeding of sire and dam and also as regards the elimination of young at birth. The improvement of C0 over the inbreds shown in Figure 9 thus measures directly the effect of the crossbreeding of the young themselves. The level of random-bred stock is reached immediately. The record of Experiment CA, also inbred dam, crossbred young, is even higher. The fact that the records are no higher in Experiments CC and AC, in which the young are equally crossbred and the dam also is crossbred, might be taken as indicating that the breeding of the dam is of no importance whatever in the rearing of the young. This conclusion, however, is not really warranted by the data. It will be remembered that there was a distinctly heavier elimination at birth in Experiments C0 and CA

than in CC and AC. Thus the dams with living young in the former experiments were a more selected sample than those of the latter. It seems probable, then, that there really is a relation between the breeding of the dam and success in rearing the young, but that it is masked in the present case by an interrelation with the mortality at birth.

The records of the inbred families are interesting in this connection. There is considerable variation, which, as shown in the previous paper, is significant and persists from year to year. The two poorest families in rearing the young (39 and 32) were the two best in percentage alive at birth, while the poorest in the latter respect (2) is next to the best in rearing the young. There is here a suggestion of a negative interrelation ($r = -0.60$). It has been shown, however (part II, Bulletin 1090), that in two earlier periods when 23 families were on hand there was no significant correlation between the records in these two respects ($r = +0.03$ for 1906–1910 and $r = +0.30$, 1911–1915). As indicated in the above paper, we probably have an unstable balance between the influence of certain genetic factors which tend to bring about a positive correlation and the tendency toward a negative correlation due to the influence of selective mortality at birth on postnatal mortality.

The record of Experiment C1 is somewhat below that of CC. It is of course expected that a decline will be shown in the first generation of renewed inbreeding in a character in which the breeding of the young is a factor. If the breeding of the dam were of no importance at all, the record of C1 should be only half as much above the inbreds as CC. The relatively small decline of C1, especially in view of its unexpectedly high record in percentage born alive, is thus evidence that the breeding of the dam does count. There is a further decline in Experiment C2, where both parents and young are inbred. As will be explained later, the record of C2, whether due to dam or young or both, should be just halfway between the inbreds and CC.

The records of CG and CL are somewhat lower than expected but still above the best of the inbred families. Here again it is shown that the condition of young at weaning gives no indication of their success later as parents.

The mortality between birth and weaning is shown separately for each size of litter in Figure 21. The results agree with those obtained from the use of indices.

Summing up, the mortality between birth and weaning depends primarily on the characteristics of the dam. A much larger percentage are raised among crossbreds in all sizes of litter than in the best of the inbred families. The apparent thriftiness of the parents when they themselves were weaned gives no indication of the mortality to be expected among their young.

THE PERCENTAGE RAISED OF ALL YOUNG BORN.

The percentage raised of all young born is simply the product of the two which we have been considering. Figure 10 brings out the superiority of crossbred young from inbred dams (CO, CA) over inbreds, and the still greater superiority of crossbred young from crossbred dams (AC, CC). The record of the first generation inbreds from crossbred dams (C1) is a little higher than theory would indicate. There is, however, a decline in the next generation of renewed inbreeding (C2) of almost the expected amount. It is noteworthy that the record of the random-bred stock (B) is practically reached by crossbreeding involving only three or four of the inbred families.

One of the most striking results is the great advance of the crossbreds over the best of the inbred families. The superiority of the best inbred family over the average is increased more than fourfold.

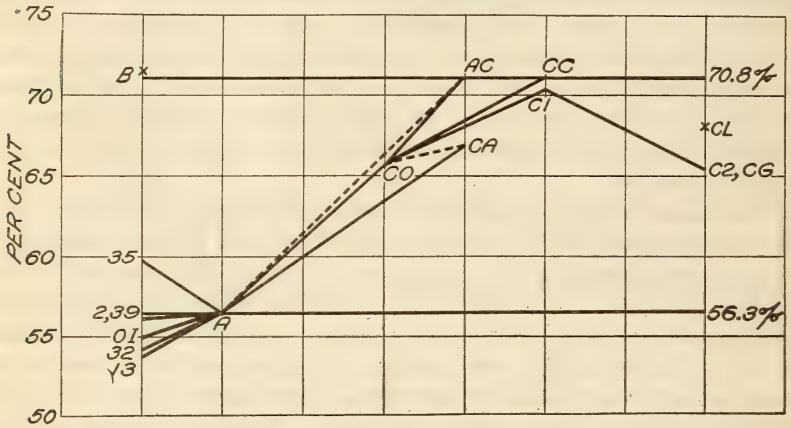

FIG. 10.—The percentage raised to 33 days of all young born, 1916–1919. Indices correcting for effects of size of litter and seasonal conditions. (See Fig. 8 for explanation of symbols.)

This is a much greater relative increase than shown in the case of either component percentage. The reason is easily discovered. An inbred family which is above the average in percentage born alive is perhaps more likely than not to be below the average in the percentage of these raised. It thus comes about that there is no more differentiation among the families in the total percentage raised than in either component. The second generation crossbreds, on the other hand, are superior in both components and thus very much superior in the product. We have here a good illustration of the way in which a great superiority of a crossbred stock over the best of its ancestral inbred families with respect to a complex character may be built up out of mere dominance of vigor over weakness in a number of more elementary characters which are distributed at random among the inbred families. Further illustration of this point will be taken up later.

BIRTH WEIGHT.

Figure 11 shows how the various experiments compare with respect to birth weight. On the whole there is considerable similarity to the situation with respect to percentage born alive (Fig. 8). In both cases the records of inbred females, however mated (inbreds, C0, CA) are poor compared with those of crossbred females (AC, CC, C1). Again there is a marked decline in both cases in the second generation of renewed inbreeding.

This similarity may be due in part to a direct causal relation. Stillborn young are naturally considerably lighter than young born alive. The high birth weights of the progeny of crossbred dams might thus be due merely to their relatively small percentage of stillborn young. This complication is avoided by comparing the birth weights of only those young which reach 33 days (Fig. 12). We find, in fact, that

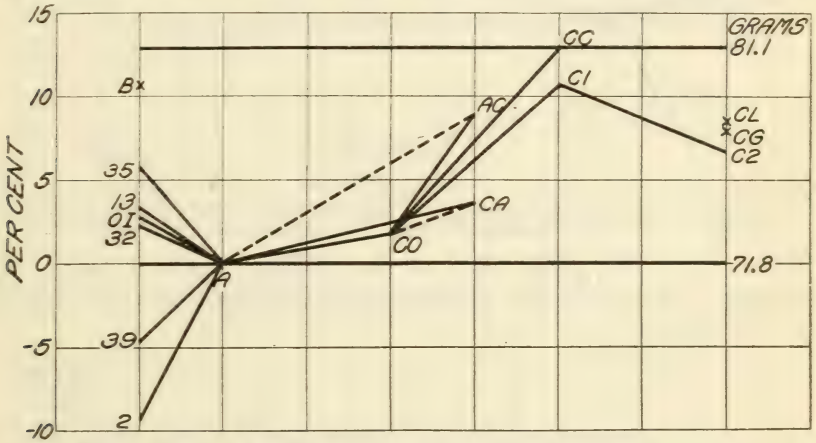

FIG. 11.—The birth weight of all young born, 1916–1919. Indices correcting for effects of size of litter and seasonal conditions (Table 2). (See Fig. 8 for explanation of symbols.)

the differences among the experiments are reduced. Nevertheless the essential points noted above are still present. It seems clear that the prenatal rate of growth depends largely on the characteristics of the dam as far as it depends on heredity at all. The heredity of the young, however, seems to be more important than in the case of the percentage born alive, as indicated by the records of Experiments C0 and CA in comparison with the inbreds. That the agreement in the standing of the crossbreeding experiments in relation to the total inbreds in the two respects, birth weight and percentage born alive, does not rest on a common physiological factor is shown by the lack of agreement among the separate inbred families.

Experiment CG, in which the parents were selected because of their exceptionally great weight at weaning, produced heavier young than Experiment CL, in which the parents were underweight at the same age. Even CL, however, is well above the average of the inbreds

while CG is no better than the second generation crossbreds. It is not safe to conclude that the selection for weight has had any effect.

The birth weights of the young raised in the inbred families and in Experiments C0, CC, C1, and B are compared for each size of litter

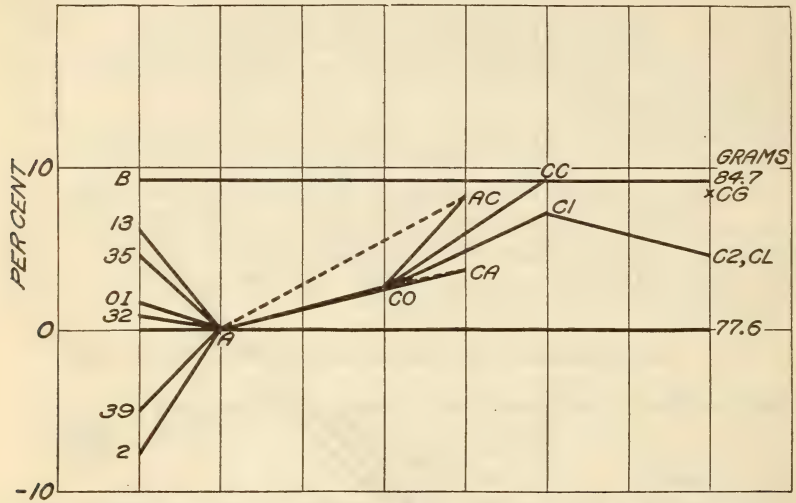

FIG. 12.—The birth weight of the young raised to 33 days, 1916–1919. Indices correcting for effects of size of litter and seasonal conditions (Table 2). (See Fig. 8 for explanation of symbols.)

in Figure 22. The great effect of size of litter on birth weight is illustrated. Otherwise the conclusions are the same as those drawn from the indices.

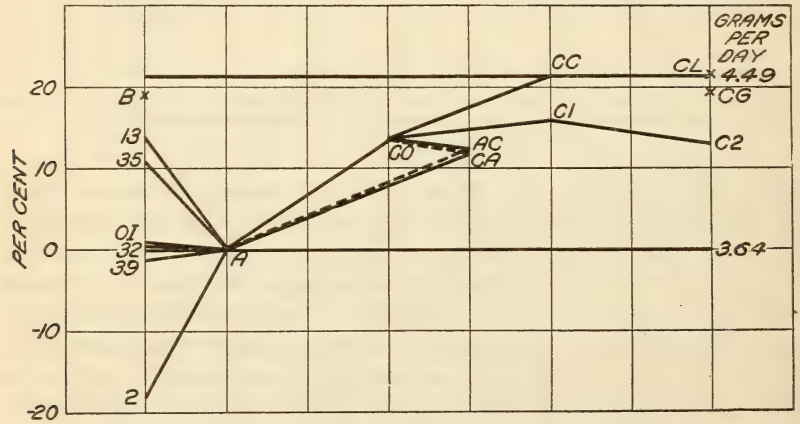

FIG. 13.—The rate of gain between birth and 33 days, 1916–1919. Indices correcting for effects of size of litter and seasonal conditions (Table 2). (See Fig. 8 for explanation of symbols.)

DAILY GAINS.

We have seen that the results for birth weight are similar to those for percentage born alive. The results for daily gain between birth and weaning (Fig. 13) are, on the other hand, more like those for

percentage raised of the young born alive. The superiority of the crossbreds produced by inbred females (C0, CA) over inbreds shows that the heredity of the young counts for a great deal. The still greater superiority of the crossbreds from crossbred parents (CC) shows, however, that the breeding of the dam is also of much importance, as would of course be expected. The effects of renewed inbreeding may be seen in the lower average of C1 as compared with CC and the still lower average of C2. The result of crossing inbred male with crossbred female (AC) is practically the same as the reciprocal cross (CA). One would expect an average as high as CC. There seems to be no explanation other than an extreme chance deviation.

The young from crossbreds selected for their rapid gains (CG) did not show as great a percentage advance over the inbreds as the young

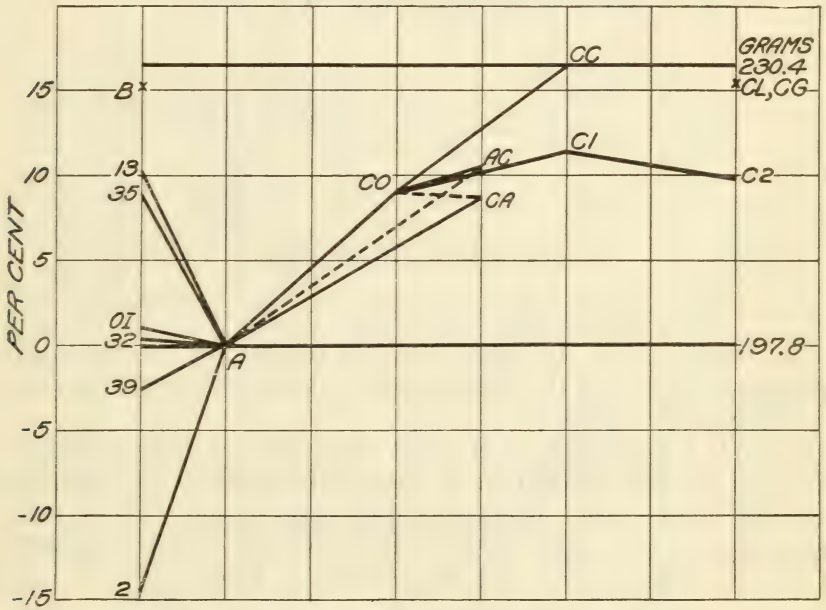

FIG. 14.—The weight at 33 days, 1916–1919. Indices correcting for effects of size of litter and seasonal conditions (Table 2). (See Fig. 8 for explanation of symbols.)

from the subnormal parents in Experiment CL. We again conclude that direct selection is futile in the case of characters of the kind dealt with here, in which hereditary differences are small compared with those due to environment.

The comparison of the gains of the inbreds C0, CC, C1, and B in separate sizes of litter (Fig. 23) confirms the results from the indices.

WEIGHT AT WEANING.

This is merely the sum of the birth weight of the young raised and the gain from birth to 33 days (Fig. 14). As it depends largely on the latter factor, no additional points of interest are brought out.

ADULT WEIGHT.

The complete growth curve has been studied in those animals which have been saved beyond 33 days. The details will not be discussed in the present paper. It may be said, however, that a pronounced effect of crossbreeding is observable in the first generation of crossing and that about half of the increase is lost in the first generation of renewed inbreeding.

Table 8 shows the average weights of males and females in the five large inbred families and in the random-bred stock, 1916 to 1919 inclusive, taken at the time of recording a litter at the ages of 12 or 13 months. The females are thus not pregnant.

TABLE 8.—*Average weights at 12 or 13 months (1916–1919); taken after birth of litter, inbreeding experiments and random-bred stocks.*

Family.	Males.		Females.	
	Number.	Weight (grams).	Number.	Weight (grams).
2	36	716± 6.9	35	625± 5.3
13	31	845± 9.2	33	686±11.1
32	20	700±10.1	21	649± 7.8
35	32	770±10.4	32	669± 8.6
39	16	757±17.0	14	653±19.1
Total inbred	135	761± 5.4	135	657± 4.5
B	58	852± 9.9	60	700± 7.9

The superiority of the males over the females, of the crossbreds over the inbreds, and the differentiation among the inbred families, are brought out.

In Table 9 animals from the first cross between inbred families, and from the first generation of renewed inbreeding, are compared with the inbreds used in crossbreeding experiments. As in Table 8, the weights were taken at 12 or 13 months of age after the birth of a litter. These inbreds are not included in Table 8.

TABLE 9.—*Average weights at 12 or 13 months (1917–1920); taken after birth of litter. Animals used in crossbreeding experiments.*

Experiment.	Males.		Females.	
	Number.	Weight (grams).	Number.	Weight (grams).
Inbreds (in CO, AC, CA)	95	776 ± 6.4	91	641 ± 4.8
CO (in CC, C1, CA, AC)	77	865 ± 8.8	82	726 ± 6.6
C1 (in C2)	9	824 ±13.2	9	667 ±17.5

It will be seen that the first cross (CO) results in an increase of 12 or 13 per cent in adult weight, but that at least half of this is lost

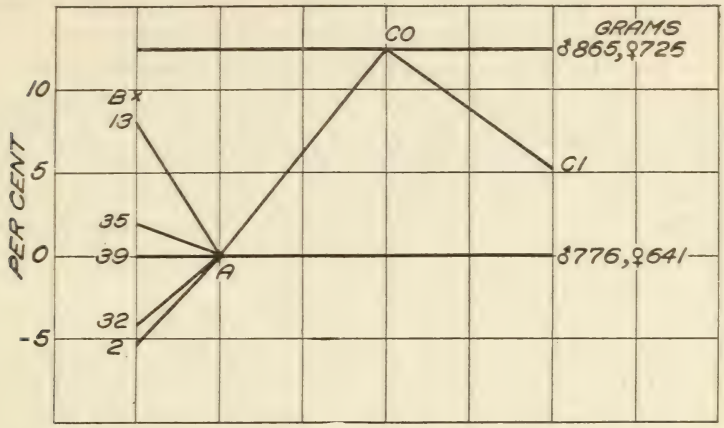

FIG. 15.—Adult weight, 1917-1920. Comparison between inbred families (2, 13, 32, 35, 39), total inbreds (A), random-bred stock (B), first cross (C0), and first generation of renewed inbreeding (C1). Percentage differences for males and females averaged. (See Table 9.)

on renewing inbreeding (C1). Figure 15 brings out these points graphically.

FREQUENCY OF LITTERS.

It is conceivable that the heredity of the fetuses might make a difference in the number of litters completely absorbed or aborted at

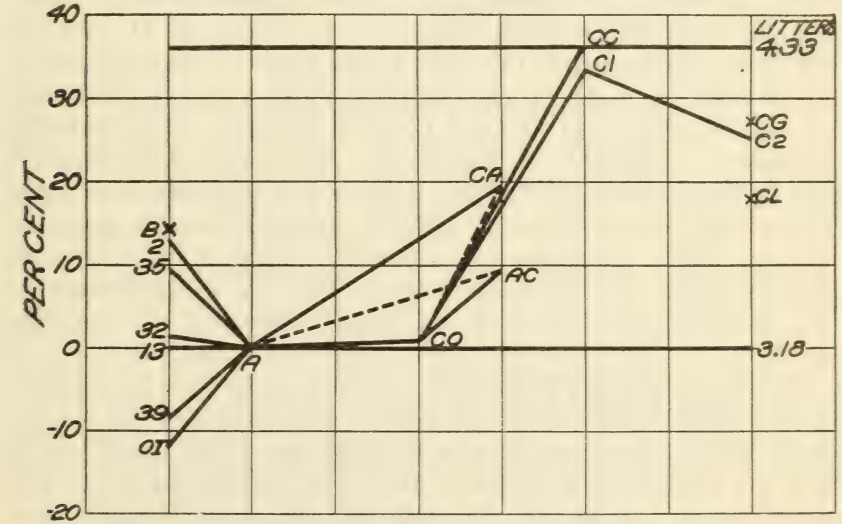

FIG. 16.—Regularity in producing litters (litters per mating per year), 1916-1919. Effects of seasonal conditions eliminated (Table 2). (See Fig. 8 for explanation of symbols.)

an early stage, and thus make a difference in the frequency of recorded litters. As it turns out, however, the frequency of litter (Fig. 16) is

virtually identical in the cases of inbred females mated respectively with brothers (young inbred) and with unrelated inbred males (C0).

When the crossbred young themselves become parents there is a marked increase in the regularity with which litters appear. The result is practically the same whether these crossbred parents are unrelated (CC) or brother and sister (C1), again indicating that the vigor or weakness of the young is not a factor. A falling off appears when the parents are from the first generation of renewed inbreeding (C2). In these respects there is considerable similarity in the results shown in Figures 8 and 12, dealing with percentage born alive and birth weight, respectively, characters which we concluded were largely dependent on the dam.

There is, however, a striking contrast with those cases in the standing of Experiments CA and AC. The great increase in frequency of litter when a crossbred male instead of an inbred is mated with an inbred female (CA) seems to mean that the sire is most apt to be responsible for irregularity in producing litters. The mating of inbred males with crossbred females (AC) however gives a better record than where both parents are inbred. This indicates that the female is also responsible to some extent. The still greater improvement where both parents are crossbred (CC, C1) substantiates further the responsibility of both parents.

It should be recalled here, however, that Experiments CA and AC are compared with inbreds during a period when the latter were producing litters more frequently than the inbreds breeding simultaneously with CC and C1. The actual records of AC and CA were only slightly below CC and C1 and were so near the upper limit possible for a guinea pig (which is about 5.3 litters per year) that the superiority of CC and C1 over CA and AC is probably somewhat exaggerated in Figure 16. The same considerations apply to Experiments CG and CL, which would probably have made records more nearly like CC and C1 under strictly comparable conditions. The main conclusion that frequency of litter depends primarily on the sire and secondarily on the dam is not weakened.

Another important result is the great superiority of crossbreds derived from only two inbred families over the random-bred stock. In the other characters with which we are dealing there is merely a recovery of the condition of the latter. It is probably not a coincidence that frequency of litter is the only one of our characters in which the miscellaneous inbred families (OI) are inferior to the five largest families (2, 13, 32, 35, and 39). It seems probable that regularity in producing litters has been the most important factor in the unconscious natural selection among the inbred families and that the crossbreds are in this case derived from a selected ancestry. The possibility of improvement in all characters through conscious

selection from a group of inbred lines, followed by crossbreeding, is clearly indicated. The method is especially applicable to characters such as those used here, in which heredity is such an insignificant factor in individual cases that selection of individuals is of no value.

AGE OF MATURITY.

It was thought at first that the influence of the sire on frequency of litter as here measured might be due to earlier maturity of crossbred males. Females, as noted previously, may become capable of reproduction at one month of age, while males only begin to mature at about two months. If crossbred males mated at weaning were able to produce a litter in advance of the inbred males, they would produce more litters in the first year of mating even though there were no greater regularity after their first litter. However, a tabulation of the ages of the males at birth of their first litters (Table 10) shows that earlier maturity of the males does not explain the superiority of CA over AC. Their first litters were produced at nearly the same age, (5.09 and 5.03 months). The superiority of all crossbreeding experiments (except C0) over the inbreds seems, however, to be in part explained by earlier maturity of the parents.

TABLE 10.—*Average age of males, mated when 1 or 2 months of age, at birth of their first litter, and average interval from mating to first litter in case of males 3 months old or over when mated. First litters born 1916–1919.*

Experiment.	Male mated at 1 month.		Male mated at 2 months.		Male 3 months or over.	
	Number.	Average age at first litter.	Number.	Average age at first litter.	Number.	Average interval to first litter.
2	62	5.84	1	5.00	5	3.20
13	55	5.80	0	.....	2	3.00
32	40	5.78	1	5.00	3	4.00
35	76	5.40	0	.....	2	5.50
39	25	6.28	0	.....	6	4.50
Other	84	6.18	0	.....	0	.....
Inbred	342	5.85	2	5.00	18	4.00
C0	94	5.73	33	6.06	30	4.17
CA	35	5.09	4	5.50	3	4.33
AC	30	5.03	7	5.43	9	3.67
CC	20	4.90	20	5.40	4	3.50
C1	46	5.09	5	5.80	0	.....
C2	17	4.77	2	5.00	0	.....
CL	29	5.21	6	5.17	4	3.25
CG	40	4.68	10	5.20	0	.....
B	20	5.05	29	5.48	48	4.23

Apparently the females, which were in all cases of practically the same age as the males at the first litter, were also in part responsible for the delay in the first litter of inbreds. The relatively early age of first litter in AC proves this.

One interesting side light is the remarkably early average age at first litter in Experiment CG (4.68 months) and the greater age in CL (5.21 months) as compared with most of the other crossbreeding experiments. We have here the clearest case of a difference between these experiments due to selection. The unusually heavy animals

in CG produced a litter two weeks earlier than the small-sized animals of CL selected because of birth in a large litter.

An unexpected result is shown in the last column in the long interval between mating and first litter when the animals were already 3 months or more of age at mating. Compare especially the age of 5.05 months at which weanlings in Experiment B produced their first litter with the interval of 4.23 months between mating and first litter in the case of parents already mature at the time of mating.

COMPLETE STERILITY.

There has not been much complete sterility in any stock, inbred or crossbred. Among 335 matings of inbreds which were kept for at least one year after maturity, only six failed to produce young. Three of these were kept through a second full year and continued sterile. Two of them belonged to Family 36, one to Family 17, while the other three were in Experiment C0, two being matings

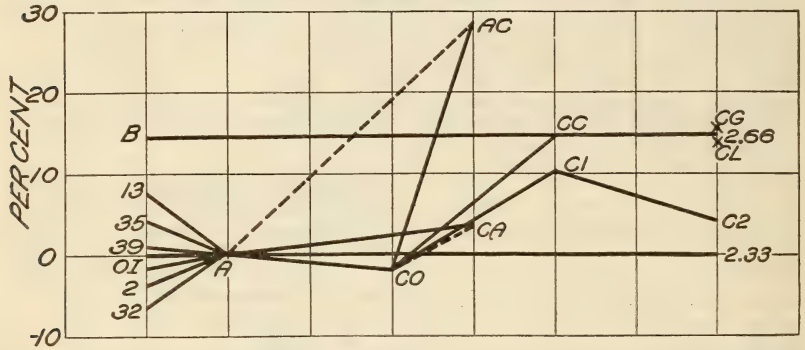

FIG. 17.—Average size of litter, 1916–1919. Effects of seasonal conditions eliminated (Table 2). (See Fig. 8 for explanation of symbols.)

between a male of 38 and a female of 13 and the other between a male of 39 and a female of 32. Among 234 matings in which one or both of the parents were crossbred and which were kept for more than 12 months, only two failed to produce young.

SIZE OF LITTER.

In the study of the size of litters the heredity of the young is again shown to be of no account by the comparison (Fig. 17) between the inbreds and the first cross (C0). The superiority of Experiment CA over C0 is so slight ($1.5 \times PE$) that it can not be taken as evidence that crossbreeding of the sire has any influence on size of litter.

The reciprocal cross, inbred male by crossbred female, however, gives such a great increase that there can be no question about the effect of crossbreeding of the dam on her fecundity.

The effect of crossbreeding of one of the parents, presumably the dam, is shown by the records of Experiments CC and C1. But the

fact that these experiments gave very much less increase than AC confronts us with something of a puzzle. The difference is too great to be dismissed as due to chance ($5.8 \times PE$). The probable explanation is a reciprocal physiological relation between frequency and size of litter. It has, in fact, been found in the inbred stock that when one litter follows immediately after another (i. e., in 9 or 10 weeks, the gestation period), it is smaller than the average, and that a large litter predisposes toward a delay before the appearance of the next litter. (See Part I, Bulletin 1090.) These negative relations were not very strong, and in the more vigorous random-bred stock the relations were positive. We doubtless have, however, as suggested in the case of the relations between mortality at birth and mortality between birth and weaning, an unstable balance between opposed influences. It was shown in Part I that the records of the inbred and control stocks rose and fell in parallelism from year to year in these two elements of fertility (as well as in all other elements of vigor). In the present paper it is shown that there is considerable agreement between frequency and size of litter in the rise and fall from season to season during 1916 to 1919 (Figs. 4 and 5). Thus external conditions tend to produce a positive correlation. There may also be common genetic factors which tend the same way. The apparent conflict between the evidence from random-bred and inbred stocks, referred to above, merely means that in the random-bred stock the causes of positive correlation were not completely balanced by the reciprocal physiological relation suggested above, while it was overbalanced in the inbred stock. One would expect to find the physiological relations more important in the weaker inbred stock.

In comparing AC with CC or C1 we have experiments in which the inherent characters of the dam and young are essentially the same. Owing, as it appears, to the influence of the crossbred sire, CC and C1 produced litters distinctly more regularly than did AC. We have here a situation in which a negative physiological correlation could reveal itself uncomplicated by any positive correlation. The high record of AC relative to CC and C1 in size of litter and the opposite relations in frequency of litter are the expected results on this hypothesis.

Similarly the relatively high record of CA in frequency of litter may exert a slight depressing influence on its record in size of litter. The argument that the sire exerts some influence on size of litter is strengthened, but hardly enough to be relied upon.

We may conclude that crossbreeding causes a marked increase in the size of litters produced by females. Crossbreeding of the sire may have some influence, but too slight to be demonstrated by the present data. The heredity of the young appears to be wholly without influence. It may be added that selection of the dams (and

sires) from large litters (CL) or from small litters (CG) is without effect.

TOTAL FERTILITY.

The number of young born per mating year (Fig. 18) is merely the product of the two elements of fertility, frequency and size of litter,

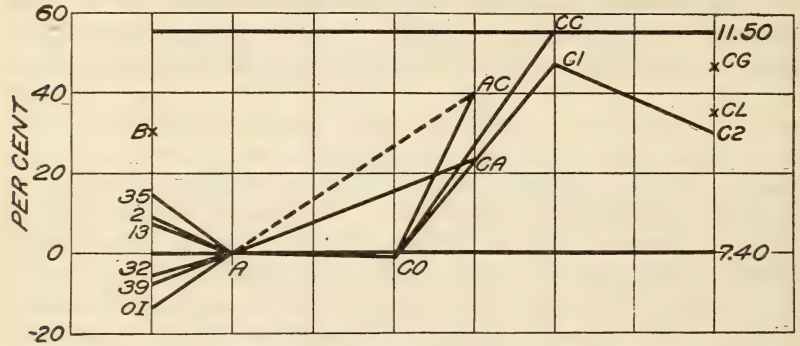

FIG. 18.—Young per mating per year, 1916–1919. Effects of seasonal conditions eliminated (Table 2). (See Fig. 8 for explanation of symbols.)

which we have discussed separately. It is interesting to find that the dam has more influence on total fertility than the sire, in spite of the greater influence of the latter on frequency of litter. Selection

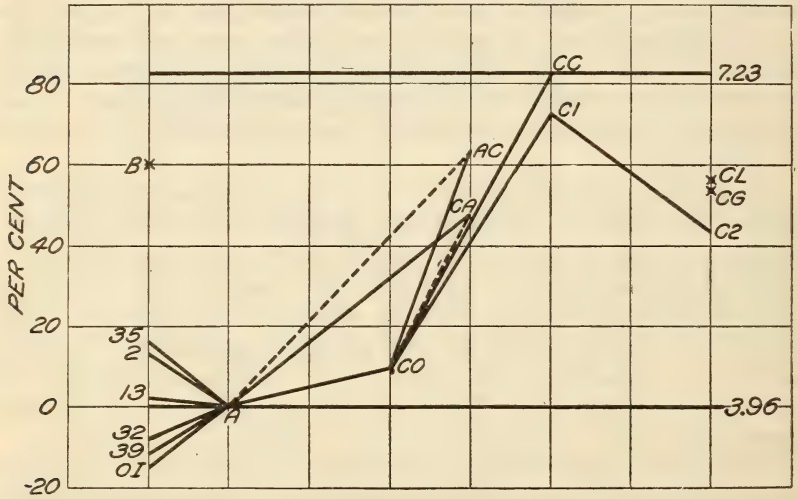

FIG. 19.—Young raised per mating per year, 1916–1919. Effects of seasonal conditions eliminated (Table 2). (See Fig. 8 for explanation of symbols.)

of parents on the basis of size of litter is shown to be wholly without effect.

The best single measure which we have of the reproductive efficiency of the experiments is the number of young raised per year. This is the product of the young born per year and the percentage raised to 33 days (actual, not index). Figure 19 shows the tremendous advance

(more than 80 per cent) obtained in the second generation of crossbreeding over the average of the inbred families. The record of the original random-bred stock is surpassed by nearly 15 per cent by

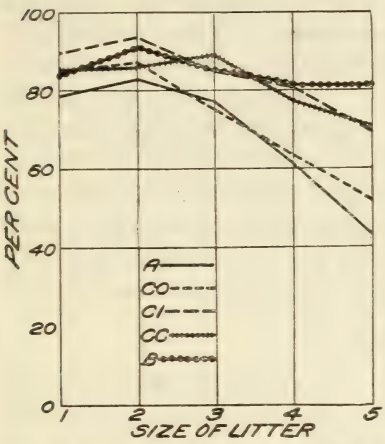

FIG. 20.—The percentage born alive, by size of litter (Table 15), 1916–1919. (See Fig. 8 for explanation of symbols.)

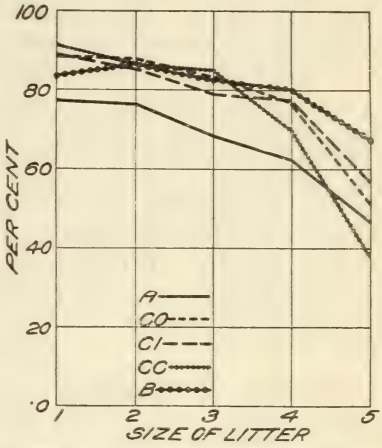

FIG. 21.—The percentage raised of the young born alive, by size of litter (Table 16), 1916–1919. (See Fig. 8 for explanation of symbols.)

Experiment CC. In fact, it was merely necessary to cross two inbred families and obtain a second generation (C1) to obtain an advance of 70 per cent over the inbred ancestry and go beyond the random-bred stock.

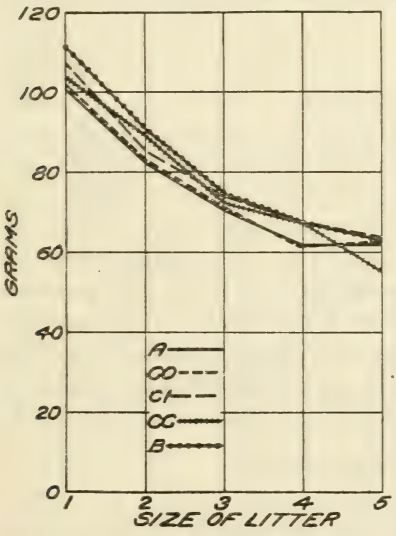

FIG. 22.—The birth weight of young raised to 33 days, by size of litter (Table 19), 1916–1919. (See Fig. 8 for explanation of symbols.)

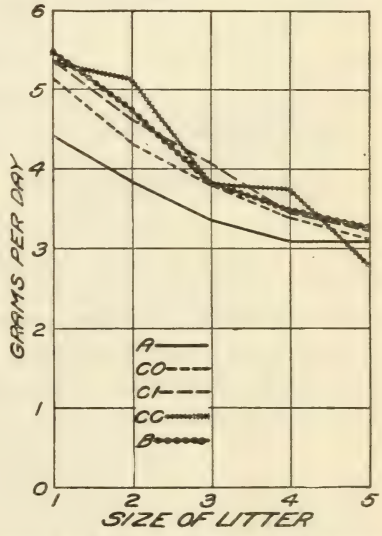

FIG. 23.—The rate of gain per day by size of litter (Table 20), 1916–1919. (See Fig. 8 for explanation of symbols.)

Another important result is seen in comparing the advance of 80 per cent in Experiment CC with the 16 per cent by which the best inbred family differs from the average. Looking at this result alone,

it seems difficult to believe that the superioity of the crossbreds is due merely to dominance of factors present in some of the inbred families, but absent in others, the hypothesis which will be at the basis of our later discussion. We are, however, able to analyze the character which we are considering into four components. The crossbreds do not exceed the best inbred family to anything like as great an extent in each of these component characters. The superiority of the crossbreds is consistent, however, and hence cumulative, in comparison with the superiority of the best inbred family over the average, the "best" inbred family being one family in one case and another in another. The four component characters are themselves doubtless highly complex genetically. If further analysis were possible, it might well turn out that dominance of the factors tending toward vigor in each respect is not even perfect.

COAT COLOR.

Six series of Mendelian factors are known which affect color in guinea pigs. Among our five leading inbred families there are variations in only two of these series, the albino series (C, c^k, c^d, c^r, c^a) and the agouti series (A, a', a). All five families are piebald (s) instead of self (S), tortoise shell (e′) instead of self-black (E) or self-red (e), black (B) instead of brown (b), and black (P) instead of pink-eyed pale sepia (p).

TABLE 11.—*Color pattern and factorial composition of the five principal inbred families.*

Family.	Color.	Factorial composition.
2	Black-red-white tricolor	CCaa.
13	Black-red-white tricolor	CCaa.
	Occasional albinos	c^ac^aaa.
32	Agouti-red-white tricolor	CCAA.
35	Yellow agouti-yellow-white tricolor	c^kc^kAA.
39	Agouti-red-white tricolor	CCAA.

First crosses between Families 2 and 13 produce black-red-white tricolors. All other first crosses among these five families produce agouti-red-white tricolors, except that occasionally cream agouti-cream-white tricolors (c^kc^aAa) appear in crosses between Families 35 and 13. Segregation takes place in regular Mendelian fashion in later generations, there being no linkage between factors C and A.

RESISTANCE TO TUBERCULOSIS.

Experiments conducted cooperatively by the Bureau of Animal Industry and Dr. Paul A. Lewis, of the Henry Phipps Institute, have been described in another paper (Wright and Lewis, 1921).

It was found that there was very little relation between age, weight, rate of gain, or sex, and the length of life after inoculation with tuberculosis. These factors combined determined less than 7 per cent of the variation in a very heterogeneous lot.

On the other hand, marked differences were found among the inbred families. Family 35, the most resistant, lived about twice as long after inoculation, on the average, as the poorest family, No. 39. Family 2 is second in resistance, Family 32 third, and Family 13 fourth.

Families 35 and 2 are superior to the random-bred stock B in this respect.

Crosses between families produce young which are in general at least as resistant as the better parent family. In particular cases the young are distinctly more resistant than either parent family. There is thus dominance of resistance over susceptibility and in particular cases each parental family supplies something lacking in the other.

Comparisons between Experiments CO, CA, and AC indicate that the full effect of crossbreeding is manifest in the first generation. The degree of resistance is determined by the genetic composition of the animal itself, the sire or dam being without direct influence.

EARLY VIEWS ON INBREEDING.

The general character of the results which have been obtained in the present experiments have little novelty. Inbreeding has been practiced by innumerable livestock breeders, in some cases merely because it was the path of least resistance, in other cases deliberately.

The great majority of these breeders, even those of the second class, have undoubtedly seen something like the degeneration described in the present paper—reduced size, lowered fertility, and increased difficulty in raising the young. In many cases much more serious degeneration has been encountered and the inbred line has rapidly become extinct. Conversely, the beneficial effects of outcrossing have often been observed. The popularity of the Angus-Shorthorn cross in Scotland threatened at one time to wipe out the pure Angus breed.

On the other hand, the use of inbreeding was an essential element in the success of the noted breeders, who laid the foundations of the modern pure breeds of livestock. It was to a large extent by inbreeding from carefully selected animals that they fixed the type which they desired and made it prepotent. This effect as well as degeneration finds its parallel in our experiments. We may call attention here to the unconscious fixation of color and to the isolation of important genetic differences in characters, such as weight and fertility, in which the degree of determination by heredity is too small to furnish a handle for direct selection.

Breeders thus have obtained sufficiently definite consequences following inbreeding. The question as to the effects has remained

unsettled, however, because those observed by different breeders seemed irreconcilable. There were two main theories among breeders. According to one, inbreeding has a specific detrimental effect, depending on its closeness and the length of time it is pursued, while the introduction of outside blood has a specific stimulating effect. According to the other view, inbreeding merely concentrates and intensifies the peculiarities of the given line, whether good, bad, or indifferent.

Neither of these theories was wholly satisfactory, the first because it failed to account for the success of such men as Bakewell, the Colling Brothers, Bates, Hewer, Cruickshank, and other noted breeders who practiced inbreeding; the second because it did not explain satisfactority the deterioration usually found on inbreeding a stock which appeared to combine every element of vigor.

PRE-MENDELIAN EXPERIMENTS.

The first systematic experiments on the subject were made by Darwin, who tested the effects of self-fertilization and crossing on a large number of plants. His results were closely similar in almost every respect to those which we have found on inbreeding guinea pigs. There was a similar degeneration in size, fertility, and vitality in most cases in which plants were used which are normally cross-pollinating. This degeneration did not continue indefinitely. Moreover, in some lines of a given species there would be little if any degeneration after many generations of selfing, while other lines of the same species degenerated rapidly. Crossing within a selfed line had no effect, but crosses between different lines resulted in increased vigor.

These results, the explanation of which seems clear enough to us to-day, were in some respects a puzzle to Darwin. He admitted that he was unable to formulate any complete explanation. He inclined toward the view that the degree of difference in the composition of the uniting germ cells has a specific stimulating effect. The following quotation expresses this view:

> There are two other important conclusions which may be deduced from my observations; firstly, that the advantages of cross fertilization do not follow from some mysterious virtue in the mere union of two distinct individuals, but from such individuals having been subject during previous generations to different conditions, or to their having varied in the manner commonly called spontaneous, so that in either case their sexual elements have been in some degrees differentiated. And secondly, that the injury from self-fertilization follows from the want of such differentiation in the sexual elements. These two propositions are fully established by my experiments.—(The effects of cross and self fertilization in the vegetable kingdom. London, 1876, p. 443.)

No fault is to be found with Darwin's experiments. That he was unable to formulate a thoroughgoing explanation of them was due

simply to the impossibility of such a formulation until more was known of the principles of ordinary heredity.

This same remark applies to a number of experiments on inbreeding of animals which were made before the rediscovery of Mendel's law. Crampe (1883) and Ritzema-Bos (1894) inbred rats and obtained marked degeneration in fertility and vitality. In Crampe's strain there was also considerable decline in weight and many abnormalities appeared, effects which Ritzema-Bos did not obtain. Weismann and Von Guaita bred mice brother and sister for many generations and noted a decline in fertility. Similar results were obtained by Fabre-Domengue with pigeons.

MENDELIAN HEREDITY AND THE PROBLEM OF INBREEDING.

With the rediscovery of Mendel's law, the explanation of at least one class of effects attributed to inbreeding at once became clear. It had often been noted that in the human race certain rare abnormalities, of which albinism is a good example, most frequently appeared among the progeny of consanguineous marriages. Good reasons were soon found for believing that albinism in man is a simple Mendelian recessive. A recessive factor can come into bodily expression only if it is received from both parents. A rare recessive trait is transmitted by many more people than actually show it. Nevertheless, these transmitters are relatively uncommon in the total population and the chances of union between them are not great. If, however, a given individual can transmit the trait, the chances are by no means small that a close relative will also have received the factor from the common ancestor and be a transmitter. Thus it is clear why consanguineous matings should frequently bring to light such traits as albinism. We see that inbreeding can not cause abnormalities of this kind to appear in a stock from which the genetic basis is absent. It is, however, a system of mating which is likely to reveal any abnormalities carried out of sight in the stock by recessive factors. We can see how inbreeding could lead to the frequent appearance of abnormalities in Crampe's stock of rats and yet fail to do so in the stock of Ritzema-Bos.

Castle and students (1906) inbred the fruit fly *Drosophila melanogaster* for 59 generations of brother-sister mating. While much sterility and low fertility appeared in the early generations, it was found possible to maintain high fertility by selection of lines. The segregation of recessive factors for low fertility was clearly indicated. These results have been confirmed as far as the main features are concerned in later experiments with the same fly by Moenckhaus, Hyde, and Wentworth.

Davenport (1908) called attention to the fact that in most known cases the dominant character in a pair of Mendelian allelomorphs was

the progressive one, while the recessive was retrogressive and often lacking in vigor. He pointed out that such a relation helped in understanding the degeneration sometimes but not always associated with inbreeding. This is very close to our present view. At that time, however, it was somewhat lacking in substance as a general explanation of the effects of inbreeding. The earlier work on Mendelian inheritance had naturally been confined for the most part to big, discontinuous variations. Thus the light which the Mendelian mechanism throws on the appearance of abnormalities following inbreeding was, as above stated, quickly recognized. It was not clear at first that any light was thrown on the relatively slight decline in size, fertility, and constitutional vigor which are more typical consequences of inbreeding. It was necessary to reach the viewpoint that hereditary differences may be due to a summation of the effects of numerous individually insignificant Mendelian units and that, indeed, the Mendelian mechanism is the universal mechanism of heredity under sexual reproduction.

The independent experiments of G. H. Shull and East with corn marked a big advance in adding substance to the general theory of heredity along the lines indicated above, as well as to the problem of inbreeding. Shull found that on self-fertilization an ordinary, seemingly homogeneous variety of corn broke up into strains, each highly uniform and differentiated from the others in numerous minute characteristics. There was more or less decline in size and productivity in all strains in the earlier generations of selfing, but stability was soon reached. On crossing these strains with one another there was in general a return to the original vigor.

All of these things had been observed by Darwin. On the basis of the new knowledge of heredity, however, Shull was able to show how everything could be explained on the assumption that an ordinary variety of maize is really a complex hybrid and that self-fertilization automatically isolates the various pure biotypes or "elementary species" through the segregation of Mendelian homozygotes, with the help of the additional assumption that the hybrids are more vigorous than the pure strains.

East obtained the same results and independently reached essentially the same conclusions. He suggested that there was a physiological stimulus to development in proportion to the degree of difference between the uniting germ plasms. This means in proportion to the amount of heterozygosis in some or all of the factors.

This view was contrasted with the older hypothesis which soon after was brought up again by Bruce and by Keeble and Pellew, that the vigor of crossbreds is due to dominance of factors conducive to vigor. Keeble and Pellew described experiments in which a cross between two pure strains of the pea produced hybrids taller than either, while

the segregation in the second generation proved that each strain furnished a dominant factor lacking in the other. In this case the factors were visibly different in effect, in that one increased the number of internodes, the other their length.

The two hypotheses are not easy to distinguish. Under both of them the departure from the condition of the pure inbred strains is in direct proportion to the amount of heterozygosis in at least certain factors. Under the stimulation hypothesis, however, the differences in vigor may be due to factors which of themselves have nothing to do with vigor: i. e., there may be no difference between AA and aa in vigor, while Aa may be superior to both. Under the dominance hypothesis it is merely to be supposed that Aa is equal to the more vigorous of the two homozygous types. Dominance indeed need not be perfect.

Under the dominance hypothesis it should be possible to isolate inbred strains, homozygous in all factors conducive to vigor and hence equal or superior to crossbreds. This should not be the case with the stimulation hypothesis. Again, under the dominance hypothesis, the crossing of two inbred strains, followed by random breeding, should result in a population with a skew distribution as regards measurable characters, according to the expansion of $(\frac{3}{4}+\frac{1}{4})^n$ where n is the number of factors. The distribution would be symmetrical under the stimulation hypothesis.

The invariable degeneration following self-fertilization which East observed in corn, and the failure to find skew distributions as the rule in the second generation of crosses, were urged by him in favor of the stimulation hypothesis. These objections, however, were met by Jones, who continued East's experiments with corn. He pointed out that owing to the phenomenon of genetic linkage, which was known to occur in corn as well as in several other plants and animals, the consequences of the dominance hypothesis of hybrid vigor would really be much closer to those of the stimulation hypothesis in the above respects than had been recognized. It should frequently happen that detrimental recessive factors would be linked with favorable dominant ones. In these cases the homozygotes would be of the types AbAb or aBaB, while the heterozygotes would be largely AbaB. The heterozygotes, containing both dominant factors, would be superior to both homozygous types, giving a situation almost indistinguishable from that which follows the stimulation hypothesis. In this suggestion Jones did not add a new hypothesis to the theory of inbreeding; he merely pointed out the logical consequences of a phenomenon, linkage, which had already been demonstrated. The dominance hypothesis was thus greatly strengthened. Collins (1921) has recently shown that even if linkage is disregarded, the objections to the dominance hypothesis are not serious in cases in which

numerous factors are involved. In such cases inbred segregates, homozygous in all factors conducive to vigor would be rare and the degree of skewness would be imperceptible.

It may be added that even if only one or two factors are involved, the skewness in F_2 would be imperceptible if environmental influences play an important part in the variation. In the experiments on guinea pigs described in the present paper, over 90 per cent of the variation in such characters as size of litter and weight is demonstrably due to factors which are not genetic. No significant differences in skewness or even in variation can be found between inbreds and second generation crossbreds. But none is to be expected under such conditions.

Finally, the success which some livestock breeders have had with close inbreeding and which Darwin obtained in at least one case with his morning glories indicates that inbred lines are produced occasionally which are thoroughly satisfactory from the standpoint of vigor. This point has been demonstrated most conclusively in the extensive experiments of the Wistar Institute conducted by Dr. Helen D. King (1918). In this experiment a strain of rats (two lines since the seventh generation) has been inbred, brother with sister, for 22 generations. Not only has full vigor been maintained but the inbreds have actually come to surpass the random-bred stock of the Wistar Institute in size and fertility. This result she attributes to careful selection. The strain of albino rats used was doubtless also rather homogeneous to begin with. The fact remains that long-continued, intensive inbreeding is not incompatible with a high degree of vigor.[5]

It thus turns out that as far as the facts of inbreeding and crossbreeding are concerned the distinction between the hypotheses is largely one of wording. The choice between them depends on which involves the fewest unproved assumptions. So far as the writer knows, it has not been demonstrated in any specific case that a heterozygote may show an increase in vigor while the two homozygotes are indifferent. On the other hand, it has been noted repeatedly that there is a correlation among known Mendelian characters between dominance and vigor, or, looking at it from the other end, between recessiveness and deleterious effect. Collins (1921) prefers the latter form of statement as suggesting better the probable evolutionary significance of the phenomenon.

Most of the mutations known in *Drosophila* are less vigorous than the normal strain (Morgan, Sturtevant, Muller, and Bridges, 1915). They are also mostly recessive, at any rate as regards detrimental

[5] These experiments have also given a remarkable demonstration of the success of inbreeding associated with close selection, as a method of modifying a character so difficult to deal with as sex ratio. Two lines, separated in the seventh generation, were selected respectively for high and low ratio of males to females. An average sex ratio of about 122 became fixed in one line, about 82 in the other.

effects. It is logical that there should be such a relation. The chances are much greater that any mutation will be injurious than beneficial, on the principle that anything done at random to a complex mechanism will probably damage it. Even if dominant and recessive mutations occur with equal frequency, the latter should accumulate more rapidly, since they can be carried along out of the range of natural selection, while injurious dominant mutations will tend to be eliminated at once.

Thus logically we should expect to find that recessive factors would more frequently be deleterious than dominant ones, and study of the known factors shows that such a situation actually exists. Given the Mendelian mechanism of heredity, and this more or less perfect correlation between recessiveness and detrimental effect, and all of the long-known effects of inbreeding—the frequent appearance of abnormalities, the usual deterioration in size, fertility, and constitutional vigor in the early generations, the absence of such decline in any one or all of these respects in particular cases, and the fixation of type and prepotency attained in later generations—are the consequences to be expected.

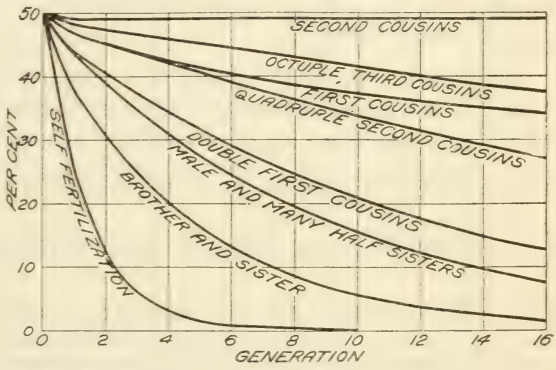

FIG. 24.—The decrease in heterozygosis in successive generations of inbreeding according to various systems of mating.

MATHEMATICAL CONSIDERATION.

The primary effect of inbreeding on this theory is the automatic increase in homozygosis. Jennings (1912) showed that with self-fertilization the percentage of heterozygotes is halved in each successive generation. The decrease following brother-sister mating was worked out by Fish (1914) and Pearl (1914). Various other systems, such as continued mating of parent with offspring, were given by Jennings (1916, 1917). A method of calculating more remote systems has been given by the writer in a previous paper (1921). Figure 24 shows the decline in heterozygosis under various systems, starting from a random-bred stock.

In Figure 24 the random-bred stock is represented as being 50 per cent heterozygous, which implies that dominant and recessive factors are equally numerous. It is easy to show, however, that the rate of decline is the same regardless of the ratio of recessive to total factors. The general formula for a random-bred population is $x^2AA + 2xy$

$Aa+y^2aa$ where x and y are the relative proportions of dominant and recessive genes. The proportion of heterozygosis in the random-bred stock is thus $2xy$. Let p be the percentage of heterozygosis after a certain amount of inbreeding. Then $\left(x-\frac{p}{2}\right)AA+pAa+\left(y-\frac{p}{2}\right)aa$ represents the composition of the population. The correlation between uniting gametes (f) comes out $1-\frac{p}{2xy}$, applying the product-moment method to the above formula. Thus $p=2xy(1-f)$. In the calculations (Wright, 1921) on which the percentages in Figure 24 are based, the formula $p=\frac{1}{2}\left(1-f\right)$ was used, which, as stated, applies to the case in which $x=y=\frac{1}{2}$. The formula for f under the various systems of inbreeding applies to any composition of the population. Thus the decline in the percentage of heterozygosis shown in the figure applies to any population provided merely that the scale is changed so that the percentage under random mating is $2xy$ instead of 50 per cent.

As regards the rate of decline in vigor (if any), it is easy to show that it is proportional to the decline in heterozygosis, regardless of the relative number of dominant and recessive genes, and regardless of the degree of dominance. In the population $\left(x-\frac{p}{2}\right)AA+p\ Aa+\left(y-\frac{p}{2}\right)aa$ the mean deviation from the dominant type is $p\ (Aa)+\left(y-\frac{p}{2}\right)(aa)$, where (Aa) represents the deviation of the heterozygotes (zero if dominance is perfect) and (aa) represents that of the recessives. The deviation in the ultimate inbred population, $xAA+yaa$, is $y\ (aa)$. Thus the deviation at any time from the ultimate level is the difference $p\ [\frac{1}{2}(aa)-(Aa)]$. This is proportional to p, the percentage of heterozygosis regardless of the values of x and y, or of the degree of dominance. Thus Figure 24 should represent the rate at which vigor declines, relative to the ultimate level, under any conditions under the various systems of mating. The absolute rate of decline, if any, depends of course on the factors in the particular case.

In comparing the theoretical with the actual rate of decline, it must of course be borne in mind that the character which is being studied must be measured on a scale such that unit differences at all parts of the range are physiologically equivalent. A correction may be necessary such as we have used in the case of percentage born alive and similar cases. In other cases a logarithmic scale may be the proper one to use (Zeleny, 1920).

We have seen that the inbred lines of guinea pigs have actually deteriorated in regard to all characters which have been studied. Unfortunately we can not make a satisfactory comparison of the rate at which this decline has taken place with theory because of the great fluctuations from year to year which are evidently due to environmental causes. We can, however, compare the records of the various crossbreeding experiments with their theoretical relations to the inbred average, since we have calculated all of them on the basis of the inbreds raised simultaneously.

Let x and y represent as before the relative proportions of any pair of factors, A and a, in the original random-bred population. We will start by assuming that the same proportions apply to the group of inbred families which are used for crossing. This implies that there has been no selection and also that enough families are taken to represent adequately the original stock. The composition of the

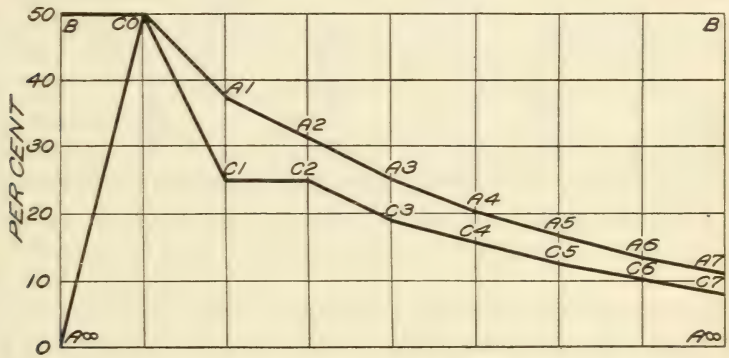

FIG. 25.—The decrease in heterozygosis and correspondingly in vigor in successive generations of inbreeding brother with sister, beginning with a random-bred stock (B, A1, A2, A3, etc.), or beginning with a first cross between homozygous lines (C0, C1, C2, C3, etc.).

first crossbred generation (CO) will then be $x^2AA+2xyAa+y^2aa$. In spite of the apparent identity with the composition of the random-bred stock, inbreeding of CO does not give the same result. This is because there is necessarily a perfect correlation between brothers and sisters in the first cross between lines assumed to have reached homozygosis, while there is a correlation of only +.50 in the random-bred stock. The results of three generations of brother-sister mating from the first cross (C1, C2, C3) are worked out in detail in Table 12 and are compared with the effects of such mating in a random-bred stock (or CC, CA, or AC) in Figure 25. There is a more rapid initial decline in vigor on starting inbreeding from the first crossbred generation. The first inbred generation (C1) is composed in part of true breeding lines (AA and aa) and in part of a group which is composed of $\frac{1}{4}AA+\frac{1}{2}Aa+\frac{1}{4}aa$, like a random-bred stock in which $x=y$, but with zero correlation between brothers and sisters. In the next generation

TABLE 12.—*Analysis of the effects of brother-sister mating following crosses between homozygous inbred lines, x of type AA and y of type aa.*

C0.					C1.				C2.				C3.			
Sire.	Dam.	AA.	Aa.	aa.	Parents.	AA.	Aa.	aa.	Parents.	AA.	Aa.	aa.	Parents.	AA.	Aa.	aa.
x *AA*	*A*	x^2			AA x AA	x^2			AA x AA	x^2			AA x AA	x^2		
									AA x AA	$\frac{xy}{8}$			AA x AA	$\frac{xy}{8}$		
													AA x AA	$\frac{xy}{8}$		
									AA x Aa	$\frac{xy}{4}$	$\frac{xy}{4}$		AA x Aa	$\frac{xy}{8}$	$\frac{xy}{8}$	
													Aa x Aa	$\frac{xy}{32}$	$\frac{xy}{16}$	$\frac{xy}{32}$
									AA x aa		$\frac{xy}{4}$		Aa x Aa	$\frac{xy}{16}$	$\frac{xy}{8}$	$\frac{xy}{16}$
x *AA*	y *aa*												AA x AA	$\frac{xy}{32}$		
													AA x Aa	$\frac{xy}{16}$	$\frac{xy}{16}$	
													AA x aa		$\frac{xy}{16}$	
			2xy		Aa x Aa	$\frac{xy}{2}$	xy	$\frac{xy}{2}$	Aa x Aa	$\frac{xy}{8}$	$\frac{xy}{4}$	$\frac{xy}{8}$	Aa x Aa	$\frac{xy}{32}$	$\frac{xy}{16}$	$\frac{xy}{32}$
													Aa x aa		$\frac{xy}{16}$	$\frac{xy}{16}$
y *aa*	x *AA*												aa x aa			$\frac{xy}{32}$
													Aa x Aa	$\frac{xy}{32}$	$\frac{xy}{16}$	$\frac{xy}{32}$
									Aa x aa		$\frac{xy}{4}$	$\frac{xy}{4}$	Aa x aa		$\frac{xy}{8}$	$\frac{xy}{8}$
													aa x aa			$\frac{xy}{8}$
									aa x aa		$\frac{xy}{4}$	$\frac{xy}{4}$	aa x aa			$\frac{xy}{8}$
y *aa*	y *aa*			y^2	aa x aa			y^2	aa x aa			y^2	aa x aa			y^2
Total....	.....	x^2	2xy	y^2	.....	$\frac{xy}{2}+x^2$	xy	$\frac{xy}{2}+y^2$	.....	$\frac{xy}{2}+x^2$	xy	$\frac{xy}{2}+y^2$	.....	$\frac{5xy}{8}+x^2$	$\frac{3}{4}xy$	$\frac{5xy}{8}+y^2$

(C2) the true breeding lines of course remain the same, while the remaining portion gives rise to a population with unchanged total composition, but with a correlation of +.50 between brothers and sisters. There is thus no difference in the percentage of heterozygosis in C1 and C2, both being just halfway between C0 and the ancestral inbred families. From this point the percentage declines as if from a random-bred stock halfway between the inbreds and the original random-breds. The percentage of heterozygosis in the later generations is about 75 per cent of its value in the same generation, starting from random-bred stock. Thus about 4 per cent of the original vigor of heterozygosis should be left after 15 generations of brother-sister mating beginning with random-bred stock, but only 3 per cent after 15 generations of such mating, following a first cross between inbred lines.

In our actual experiments only a limited number of families were used in making the crosses. This of course makes no difference in the average of the first cross (C0), provided that the particular inbred lines used are typical. By the use of selected inbred lines, on the other hand, it should be possible to produce a first cross superior to the random-bred stock.

The rate of decline on inbreeding the first cross in case an indefinitely large number of families is involved is of course merely the average of the results in particular cases. Thus the number of families used makes no difference in our conclusions as to experiments C1 and C2.

Whatever the number of families, crosses among the crossbreds in which no family is used twice, as in experiments CA, AC, and CC, are equivalent to random mating among an indefinitely large number of families. Thus the total composition and the percentage of heterozygosis should be the same in CA, AC, and CC as in C0. As already noted, however, the effects of renewed inbreeding are different.

It is only when we come to consider the effects of random mating, resumed after crossing, that we must take account of the number of families which form the foundation of the new stock. Random mating of stock derived from a small number of homozygous lines involves an appreciable amount of inbreeding and thus should give results intermediate between experiments such as C0, CC, CA, and AC, in which inbreeding is avoided, and C1, in which there is brother-sister mating. In the extreme case in which only two families are used, random mating is of course the same as brother-sister mating for one generation. There comes to be only half as much heterozygosis as in the original stock from which the two parental families were derived. The vigor of the new random breds should thus be halfway between that of the original stock and of the inbreds.

It is not difficult to find the percentage of heterozygosis under random breeding from stock derived from any given number of families. Assume that there are n families. Symbolize each family by a letter P, Q, R, S, etc. There are $\frac{n}{2}(n-1)$ different first crosses (PQ, PR, PS, QR, etc.). On commencing random breeding there is one chance in $\frac{n}{2}(n-1)$ of making a mating in which both families are used twice (like PQ×PQ) and which is thus equivalent to a mating of experiment C1. There are $2(n-2)$ chances in $\frac{n}{2}(n-1)$ of making matings in which one family only is used twice, (like PQ×QR). There are $\frac{1}{2}(n-2)(n-3)$ chances in $\frac{n}{2}(n-1)$ of making matings in which neither family is used twice, (like PQ×RS) and which are equivalent to Experiment CC. In the last case, as we have seen, there is complete recovery, on the average, of the heterozygosis of the original random-bred stock. In the first case (PQ×PQ) there is only half recovery. One might expect to find an exactly intermediate result in the case (PQ×QR), and this can easily be shown to be true by the use of path coefficients (Wright, 1921).

Since P, Q, R, and S are assumed to be completely homozygous inbred families, the constitution of the germ cells is completely determined. Thus the path coefficient from zygote to germ cell (b') is 1.0 in the first generation. As there is assumed to be no correlation between the families and hence none between their germ cells ($f'=0$), the coefficient for the degree of determination of the progeny (first cross) by germ cells (a'^2) equals $\frac{1}{2}$. For the correlation between mated individuals of the next generation we have in consequence $m=1$ in the case PQ×PQ; $m=\frac{1}{2}$ in the case PQ×QR, and $m=0$ in the case PQ×RS. For the path coefficient, zygote to germ cell, second generation, we have $b=\sqrt{\frac{1}{2}}$, by the formula $b^2=\frac{1}{2}(1+f')$. For the correlation between uniting germ cells of this generation we have $f=b^2m$. Finally, by the formula for percentage of heterozygosis, $p=2xy\ (1-f)$, we have $p=xy$ in the case PQ×PQ, $p=3/2\ xy$ in the case PQ×QR, and $p=2xy$ in the case PQ×RS. Thus the second case is exactly intermediate between the others, as we set out to prove.

Multiplying the number of matings of each kind by the corresponding percentage of heterozygosis and adding, we find the total percentage of heterozygosis in the new random-bred stock to be $100\times\frac{xy(n-1)^2}{n/2\ (n-1)}=100\times\frac{2xy(n-1)}{n}$ where $100\times 2xy$ is the percentage in the original random-bred stock. Since each pair of factors comes to equilibrium after one generation of random mating, this level of

heterozygosis will remain true indefinitely. Summing up, a random-bred stock derived from n inbred families will have $\frac{1}{n}$th less superiority over its inbred ancestry than the first cross or a random-bred stock from which the inbred families might have been derived without selection.

COMPARISON OF RESULTS WITH THEORY.

In the foregoing theoretical considerations we have assumed that the characteristics depend on the heredity of the progeny produced by the mating in question. It will be recalled, however, that we found good reason for believing that most of the characteristics in the experiments with guinea pigs were really determined wholly or in part by the parents, in most cases the dam, as far as these characteristics were genetic at all. In a character determined wholly by the dam, Experiments C0 and CA belong with the inbreds, CC, AC, and C1 represent the first cross, and C2 represents the first generation of

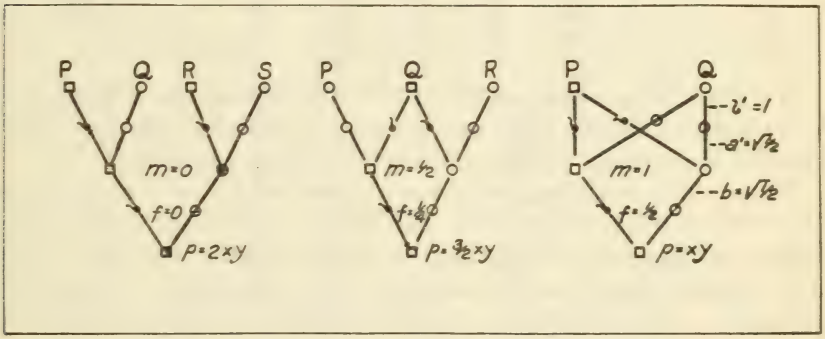

FIG. 26.—The percentage of heterozygosis following matings among inbred families of the types PQ x RS PQ x QR, and PQ x PQ. Original families, x of type AA and y of type aa.

renewed inbreeding. In characters determined partly by the parents and partly by the progeny we can easily find the relations which are to be expected by combining the expectations based on the breeding of the dam and sire with those based on the progeny. Table 13 shows the expectation in certain cases, while Figure 27 presents some of the same conclusions graphically.

TABLE 13.—*The vigor of heterozygosis to be expected in various experiments with respect to characters determined in various degrees by the sire, dam, and the animal in question.*

Character determined by—			Vigor of heterozygosis, 1 in random-bred stock, 0 in ultimate inbred stock.							
Sire.	Dam.	Young.	B.	A1.	A2.	A3.	A4.	A5.	A∞.	C0.
0	0	1	1	0.750	0.625	0.500	0.406	0.328	0	1.000
0	¼	¾	1	.812	.656	.531	.430	.347	0	.750
0	½	½	1	.875	.687	.562	.453	.367	0	.500
0	¾	¼	1	.938	.719	.594	.476	.386	0	.250
0	1	0	1	1.000	.750	.625	.500	.406	0	0
½	½	0	1	1.000	.750	.625	.500	.406	0	0
1	0	0	1	1.000	.750	.625	.500	.406	0	0

Character determined by—			Vigor of heterozygosis, 1 in random-bred stock, 0 in ultimate inbred stock.								
Sire.	Dam.	Young.	C1.	C2.	C3.	C4.	C5.	C∞.	CA.	AC.	CC.
0	0	1	0.500	0.500	0.375	0.312	0.250	0	1.000	1.000	1.000
0	¼	¾	.625	.500	.406	.328	.261	0	.750	1.000	1.000
0	½	½	.750	.500	.438	.344	.281	0	.500	1.000	1.000
0	¾	¼	.875	.500	.469	.354	.296	0	.250	1.000	1.000
0	1	0	1.000	.500	.500	.375	.312	0	0	1.000	1.000
½	½	0	1.000	.500	.500	.375	.312	0	.500	.500	1.000
1	0	0	1.000	.500	.500	.375	.312	0	1.000	0	1.000

Note that Experiments CC with the full vigor of the original stock and C2 with half this vigor are constant in position regardless of the relative importance of sire, dam, or the young themselves.

These theoretical conclusions are based solely on the hypothesis that the hereditary element in the various characters is determined wholly by Mendelian factors and that there is more tendency for the detrimental factors to be recessive than dominant. Comparison with the actual results (Fig. 27) shows that the agreement is as close as could be reasonably expected.

Adult weight and resistance to tuberculosis are examples of characters determined wholly by the young themselves. The percentage raised of the young born alive seems to be determined about three-fourths by the heredity of the young and one-fourth by the dam. In total percentage raised, rate of gain between birth and weaning, and weight at weaning, the breeding of the dam and of the young are about equally important. The data for birth weight indicate that here the breeding of the dam counts for about three-fourths, young only one-fourth or less. The percentage born alive depends almost completely on the dam. In frequency of litter, the heredity of young counts for nothing, but the sire seems to have twice as much influence as the dam. In size of litter there is complete determination by the dam. The young per year and young raised per year are merely combinations of certain of the other characters. For the last named there is something like one-eighth determination by the young.

One result which seemed rather puzzling was the relatively low record of Experiment CG, in which the parents were selected as ex-

ceptionally heavy and vigorous at weaning. In this case, as in CL, matings were made at random as far as ancestry was concerned. In many cases the same family enters into the ancestry of both parents of a given animal in these experiments. For this reason, as we have just seen, a lower record is to be expected than in Experiment CC, in which no family was used twice.

SUMMARY AND GENERAL CONCLUSIONS.

The Bureau of Animal Industry has conducted experiments for 15 years on the effects of inbreeding on guinea pigs. About 34,000 animals have been recorded. These include the records of 23 separate families, each descended from an original pair exclusively by matings of brother with sister (over 25,000 animals), a control stock

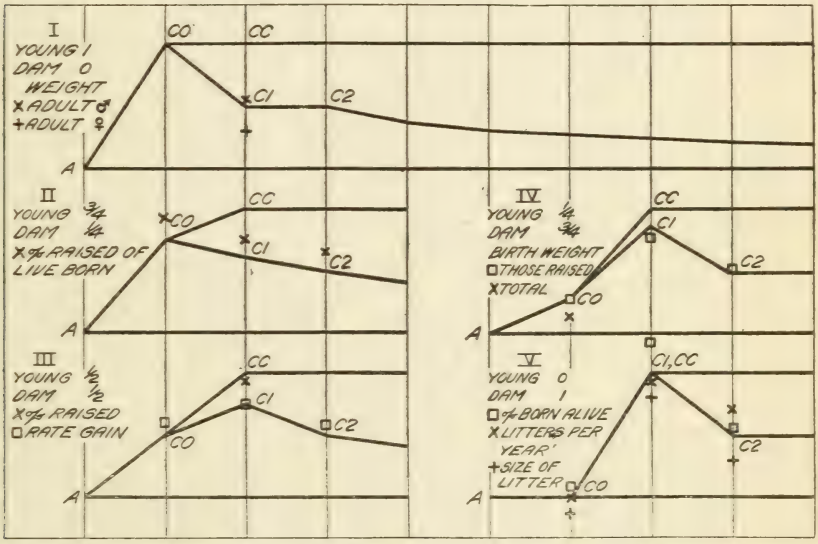

FIG. 27.—The vigor under crossbreeding (C0) and under renewed inbreeding (C1, C2, C3, etc.) relative to that in the inbred stock (A) and under continued crossbreeding (CC). Characters depending in various degrees (I-V) on dam (or sire) and young.

in which inbreeding has been carefully avoided (over 4,000 animals), and crosses among the inbred families (nearly 5,000 animals).

The fact that inbreeding of the closest possible kind has been carried on for over 20 generations in several families, without any very obvious degeneration, is a noteworthy result.

There has been on the average, however, a decline in all elements of vigor. The mortality at birth and between birth and weaning, the weight at various ages, the regularity in producing litters, the size of litter and the resistance to tuberculosis are the principal characteristics which have been studied in this connection.

Fully as important as the fact of an average decline in vigor, is the conspicuous differentiation among the families, which has been brought to light and increased by the inbreeding. This has been

most obvious in the fixation of such characteristics as color, number of toes, and tendency toward the production of particular types of abnormalities. There has also, however, been a significant differentiation in the averages made in all elements of vigor. These elements of vigor have proved to be inherited independently of each other. Each family has come to be characterized by a particular combination of traits, usually involving strength in some respects with weakness in others.

Crosses between different inbred families have resulted in a marked improvement over both parental stocks in every respect, due allowance having been made for the effects of size of litter on the other characters. This improvement appears to its full extent in the progeny of the first cross in the case of adult weight (about 12 per cent) and resistance to tuberculosis (about 20 per cent). The mortality between birth and weaning is found to depend about three-fourths on the breeding of the young and one-fourth on that of the dam. There is thus a marked improvement in the first cross (about 11 per cent) in spite of the inbred dam, but there is some additional advance in the progeny of a crossbred dam with an unrelated male. In the rate of gain between birth and weaning, the breeding of the dam and of the young are about equally important. An improvement of about 16 per cent was obtained in this respect. Birth weight depends largely on the dam—about three-fourths—and only one-fourth on the breeding of the young. There is thus only slight improvement before the second generation in which it amounted to some 9 per cent. The mortality at birth is almost wholly a maternal affair. Crossbreeding of the dam adds about 7 per cent to the chances of the young. The heredity of the young also counts for nothing in frequency or size of litter. The sire is somewhat more responsible than the dam in the former case; the dam seems to be wholly responsible in the latter. Frequency of litter was increased over 30 per cent and size of litter over 10 per cent when both sire and dam were crossbred.

The number of young raised per year by an average mating depends on four of the above elements of vigor—the mortality at birth, that between birth and weaning, and the frequency and size of litters. The relatively small improvement in crossbred matings in each separate respect as given above, is compounded into an advance of over 80 per cent in the combination, which goes well beyond the superiority of the random-bred control stock over the inbreds.

Analysis of the various crosses, indicates that the results are all the direct or indirect consequence of the Mendelian mechanism of heredity. The fundamental effect of inbreeding is the automatic increase in homozygosis in all respects. An average decline in vigor is the consequence of the observed fact that recessive factors, more extensively brought into expression by an increase in homo-

zygosis, are more likely to be deleterious than are their dominant allelomorphs. The differentiation among the families is due to the chance fixation of different combinations of the factors present in the original heterozygous stock. Crossing results in improvement because each family in general supplies some dominant factors lacking in the others. Dominance or even imperfect dominance in each unit character is built up into a pronounced improvement over both parent stocks in the complex characters actually observed.

A certain portion of the increase in vigor of the first cross between inbred families is maintained on resuming random mating. One-half of this increase is maintained in stock founded on 2 inbred lines, two-thirds in the case of 3 lines, three-fourths in the case of 4 lines, four-fifths in the case of 5 lines and so on.

It is believed that the results point the way to an important application of inbreeding in the improvement of livestock. Nearly all of the characteristics dealt with here, like most of those of economic importance with livestock, are of a kind which is determined only to a slight extent by heredity in the individual. About 70 per cent of the individual variation in resistance to tuberculosis and over 90 per cent of that in the rate of gain, and size of litter is determined by external conditions. Progress by ordinary selection of individuals would thus be very slow or nil. A single unfortunate selection of a sire, good as an individual, but inferior in heredity, is likely at any time to undo all past progress. On the other hand, by starting a large number of inbred lines, important hereditary differences in these respects are brought clearly to light and fixed. Crosses among these lines ought to give a full recovery of whatever vigor has been lost by inbreeding, and particular crosses may safely be expected to show a combination of desired characters distinctly superior to the original stock. Thus a crossbred stock can be developed which can be maintained at a higher level than the original stock, a level which could not have been reached by selection alone. Further improvement is to be sought in a repetition of the process—the isolation of new inbred strains from the improved crossbred stock, followed ultimately by crossing and selection of the best crosses for the foundation of the new stock.

This method of improvement has not been unknown in the past. In fact, most of the recognized breeds of livestock were developed, more or less unconsciously, in this way. Close inbreeding was practiced by the pioneer breeders—Bakewell, the Collings, Bates, Cruickshank, Hewer, etc. The relatively few promising families and the successful nicks between them were the foundation stock of the breeds. Further development may be expected by the intelligent application of the same principles.

TABLE 14.—*Data on the fertility in the various inbreeding and crossbreeding experiments, 1916–1919.*

Experiment.	Size of litter.							Number of mating years.	Number of litters.	Number of young.	Average size of litter.	Average litters per year.	Average young per year.	Average young raised per year.
	1	2	3	4	5	6	7							
2	87	187	133	32	2	....	....	119.3	441	998	2.26	3.70	8.37	5.00
13	45	115	85	33	12	3	....	90.7	293	740	2.53	3.23	8.16	4.30
32	60	81	63	18	1	....	....	67.8	223	488	2.19	3.29	7.20	3.91
35	64	120	108	40	9	....	....	94.9	341	833	2.44	3.59	8.78	5.11
39	39	53	51	17	2	1	....	56.3	163	382	2.34	2.90	6.79	3.39
Other	119	210	140	44	7	....	....	194.5	520	1,170	2.25	2.67	6.01	2.80
Inbred	414	766	580	184	33	4	....	623.5	1,981	4,611	2.33	3.18	7.40	3.96
C0	134	235	157	51	11	....	....	183.2	588	1,334	2.27	3.21	7.28	4.48
CA	31	57	46	23	7	....	....	39.4	164	410	2.50	4.16	10.41	7.99
AC	19	41	57	44	15	8	....	48.2	184	571	3.10	3.82	11.85	9.02
CC	42	69	82	35	9	1	....	54.3	238	617	2.59	4.38	11.36	7.61
C1	50	77	73	39	10	....	....	57.4	249	629	2.53	4.34	10.96	7.46
C2	13	31	19	10	2	....	....	17.6	75	182	2.43	4.26	10.34	7.10
CL	21	40	44	22	6	5	....	33.8	138	381	2.76	4.08	11.27	8.31
CG	32	64	56	41	13	4	....	47.4	210	581	2.77	4.43	12.26	8.16
B	81	188	212	78	21	7	1	159.6	588	1,559	2.65	3.68	9.77	6.71

TABLE 15.—*Percentage born alive.*

[Average in litters of each size, the combined average, and the index (litters of 1, 2, 3, and 4 weighted 1, 3, 3, and 1, respectively). Inbreeding and crossbreeding experiments, 1916–1919.]

Experiment.	Size of litter.							Total.	Index.
	1	2	3	4	5	6	7		
2	69.0	78.9	77.4	67.2	30.0	.....	.....	75.5	75.6
13	82.2	81.7	77.6	65.2	48.3	0.0	.....	72.7	78.2
32	86.7	90.1	76.2	61.1	0.0	.....	.....	79.1	80.8
35	70.3	89.6	78.7	63.1	42.2	.....	.....	76.2	79.8
39	87.2	85.8	81.0	60.3	90.0	100.0	.....	79.8	81.0
Other	82.4	80.2	75.5	53.4	31.4	.....	.....	73.2	75.4
Inbred	78.7	83.0	77.4	61.4	43.0	25.0	.....	75.3	77.7
C0	85.1	87.1	75.6	63.2	52.7	.....	.....	77.7	79.5
CA	87.1	86.8	86.2	80.4	71.4	.....	.....	83.9	85.8
AC	73.7	92.7	91.2	90.3	86.7	72.9	.....	88.4	89.5
CC	85.7	86.2	89.4	77.9	71.1	50.0	.....	84.1	86.3
C1	90.0	93.5	84.9	80.8	70.0	.....	.....	85.2	88.2
C2	92.3	90.3	78.9	85.0	90.0	.....	.....	85.7	85.6
CL	95.2	96.2	92.4	69.3	73.3	63.3	.....	84.3	91.3
CG	84.4	89.8	89.3	73.8	60.0	62.5	.....	80.4	86.9
B	84.0	91.0	85.4	81.1	81.0	52.4	0.0	84.2	86.8

TABLE 16.—*Percentage raised to 33 days of the young born alive.*

[Average in litters of each size, the combined average, and the index (see Table 15). Inbreeding and crossbreeding experiments, 1916–1919.]

Experiment.	Size of litter.							Total.	Index.
	1	2	3	4	5	6	7		
2	81.7	83.7	79.9	62.8	0.0	.....	.....	79.3	79.4
13	75.4	76.6	72.2	67.4	55.2	.....	.....	72.5	74.0
32	84.6	74.0	63.9	47.7	.....	.....	.....	68.7	68.2
35	80.0	79.5	78.0	71.3	36.8	.....	.....	76.4	78.0
39	76.5	74.7	61.3	39.0	55.6	0	.....	62.6	65.4
Other	70.4	70.9	53.9	63.8	45.5	.....	.....	63.5	63.6
Inbred	77.6	76.8	68.9	62.2	46.5	0	.....	71.2	72.1
C0	85.6	88.0	83.1	75.7	51.7	.....	.....	84.0	84.8
CA	96.3	92.9	89.9	89.2	96.0	.....	.....	91.6	91.7
AC	92.9	92.1	91.7	85.8	76.9	60.0	.....	86.1	91.4
CC	91.7	86.6	85.0	69.7	37.5	66.7	.....	79.6	84.5
C1	88.9	85.4	79.0	77.8	57.1	.....	.....	79.9	82.5
C2	100.0	87.5	86.7	61.8	44.4	.....	.....	80.1	85.5
CL	75.0	89.6	86.9	90.2	90.9	84.2	.....	87.5	86.8
CG	85.2	88.7	86.7	80.2	66.7	60.0	.....	82.9	86.4
B	83.8	86.3	82.7	79.8	67.1	50.0	.....	81.6	83.8

TABLE 17.—*Percentage raised to 33 days of all young, born dead or alive.*

[Average in litters of each size, the combined average, and the index (see Table 15). Inbreeding and crossbreeding experiments, 1916–1919.]

Experiment.	Size of litter.							Total.	Index.
	1	2	3	4	5	6	7		
2	56.3	66.0	61.9	42.2	0	.....	.....	59.8	60.3
13	64.4	62.6	56.1	43.9	26.7	0	.....	52.7	58.0
32	73.3	66.7	48.7	29.2	0	.....	.....	54.3	56.1
35	56.2	71.3	61.4	45.0	15.6	.....	.....	58.2	62.4
39	66.7	64.2	49.7	23.5	50.0	0	.....	50.0	54.0
Other	58.0	56.9	40.7	34.1	14.3	.....	.....	46.5	48.1
Inbred	61.1	63.8	53.3	38.2	20.0	0	.....	53.6	56.3
C0	75.4	76.6	62.8	48.5	27.3	.....	.....	65.3	67.8
CA	83.9	80.7	77.5	71.7	68.6	.....	.....	76.8	78.8
AC	68.4	85.4	83.6	78.4	66.7	43.7	.....	76.2	81.7
CC	78.6	74.6	76.0	54.3	26.7	33.3	.....	66.9	73.1
C1	80.0	79.9	67.1	62.8	40.0	.....	.....	68.0	73.0
C2	92.3	79.0	68.4	52.5	40.0	.....	.....	68.7	73.4
CL	71.4	86.2	80.3	62.5	66.7	33.3	.....	73.8	79.2
CG	71.9	79.7	77.4	59.1	40.0	37.5	.....	66.6	75.3
B	70.4	78.5	70.6	64.7	54.3	26.2	0	68.7	72.8

TABLE 18.—*Average birth weight in grams of all young, born dead or alive.*

[Average in litters of each size and the index (litters of 1, 2, 3, and 4 weighted 1, 3, 3, and 1, respectively). Inbreeding and crossbreeding experiments, 1916–1919.]

Experiment.	Size of litter.							Index.
	1	2	3	4	5	6	7	
2	86.0	72.0	60.1	50.5	44.5	.....	.....	66.6
13	101.9	80.8	68.4	59.2	50.7	39.5	.....	76.1
32	98.1	80.0	66.4	57.4	52.5	.....	.....	74.3
35	96.5	84.5	70.1	56.6	50.4	.....	.....	77.1
39	85.8	72.6	63.0	50.4	53.5	37.8	.....	67.9
Other	93.0	75.3	64.9	53.5	43.6	.....	.....	70.9
Inbred	93.0	77.0	65.3	54.7	48.9	38.9	.....	71.8
C0	97.7	77.6	64.4	53.9	48.5	.....	.....	72.2
CA	107.0	86.0	72.5	63.3	56.6	.....	.....	80.7
AC	100.3	95.8	75.7	65.9	60.3	48.8	.....	85.1
CC	101.8	86.9	70.2	59.1	51.1	71.2	.....	79.0
C1	104.2	84.4	69.8	63.5	51.7	.....	.....	78.8
C2	104.5	84.8	72.9	61.0	58.5	.....	.....	79.8
CL	104.5	90.8	78.3	66.0	56.5	53.3	.....	84.7
CG	106.7	87.5	79.0	62.8	59.2	54.0	.....	83.6
B	101.2	86.9	71.8	61.7	57.0	54.7	24.5	79.9

TABLE 19.—*Average birth weight, in grams, of young which were raised to weaning.*

[Average in litters of each size and the index (see Table 18). Inbreeding and crossbreeding experiments, 1916–1919.]

Experiment.	Size of litter.							Index.
	1	2	3	4	5	6	7	
2	94.9	76.9	65.8	58.4	.....	.....	.....	72.7
13	110.8	88.7	75.2	67.1	63.9	.....	.....	83.7
32	103.5	84.0	70.9	63.1	.....	.....	.....	78.9
35	104.5	87.3	74.4	63.6	63.1	.....	.....	81.6
39	91.1	76.4	68.3	60.8	60.5	.....	.....	73.3
Other	101.3	80.4	69.4	58.8	56.5	.....	.....	76.1
Inbred	100.9	82.1	70.4	61.9	62.0	.....	.....	77.6
C0	101.9	82.9	71.3	61.9	63.2	.....	.....	78.3
CA	110.5	89.9	74.1	69.0	60.7	.....	.....	83.9
AC	111.4	98.4	77.4	67.9	63.7	55.5	.....	88.3
CC	103.6	89.5	72.3	67.8	55.3	74.5	.....	82.1
C1	107.0	85.6	74.3	67.2	63.5	.....	.....	81.7
C2	105.3	86.7	77.6	65.0	59.5	.....	.....	82.9
CL	110.5	91.3	74.8	74.0	63.0	58.9	.....	85.4
CG	111.9	91.3	82.9	70.0	67.6	66.7	.....	88.1
B	111.5	90.8	75.0	67.7	63.0	60.0	.....	84.6

TABLE 20.—*Average daily rate of gain between birth and weaning (33 days), in grams.*

[Average in litters of each size and the index (see Table 18). Inbreeding and crossbreeding experiments, 1916–1919.]

Experiment.	Size of litter.							Index.
	1	2	3	4	5	6	7	
2	3.58	3.20	2.95	2.78	.....	.....	.....	3.10
13	5.06	4.54	3.99	3.67	3.05	.....	.....	4.29
32	4.32	4.27	3.24	2.96	.....	.....	.....	3.73
35	4.98	4.44	3.92	3.39	2.88	.....	.....	4.18
39	4.31	3.90	3.09	2.80	3.91	.....	.....	3.51
Other	4.50	3.48	2.98	2.52	2.70	.....	.....	3.30
Inbred	4.43	3.85	3.36	3.09	3.09	.....	.....	3.64
C0	5.15	4.31	3.82	3.40	3.10	.....	.....	4.12
CA	5.51	4.93	3.98	3.66	3.02	.....	.....	4.49
AC	5.49	5.06	4.23	3.53	3.45	3.77	.....	4.61
CC	5.34	5.12	3.81	3.77	2.80	5.61	.....	4.49
C1	5.36	4.63	4.07	3.46	3.24	.....	.....	4.37
C2	5.68	4.58	4.73	3.40	4.09	.....	.....	4.62
CL	6.27	5.16	4.69	4.14	2.62	3.92	.....	4.99
CG	5.80	5.20	4.63	3.90	4.04	5.20	.....	4.90
B	5.49	4.77	3.83	3.50	3.27	3.54	.....	4.35

TABLE 21.—*Average weight at weaning (33 days), in grams.*

[Average in litters of each size and the index (see Table 18). Inbreeding and crossbreeding experiments, 1916–1919.]

Experiment.	Size of litter.							Index.
	1	2	3	4	5	6	7	
2	213.2	182.4	163.3	150.2	.....	.....	.....	175.1
13	277.8	238.5	206.8	188.1	164.5	.....	.....	225.2
32	246.1	225.0	177.7	160.9	.....	.....	.....	201.9
35	269.0	233.8	203.6	175.6	158.0	.....	.....	219.6
39	233.3	205.1	170.3	153.2	189.5	.....	.....	189.1
Other	249.8	195.1	167.7	142.1	145.5	.....	.....	185.0
Inbred	247.1	209.0	181.4	163.8	164.0	.....	.....	197.8
C0	271.7	225.1	197.5	174.0	165.5	.....	.....	214.2
CA	292.9	252.7	205.4	189.8	160.3	.....	.....	232.1
AC	292.6	265.5	216.9	184.3	177.5	179.9	.....	240.5
CC	279.8	258.6	198.1	192.1	147.8	259.5	.....	230.3
C1	284.0	238.5	208.5	181.3	170.5	.....	.....	225.8
C2	292.8	237.7	233.6	177.1	194.5	.....	.....	235.5
CL	317.5	261.6	229.6	210.6	149.5	188.3	.....	250.2
CG	303.4	263.0	235.7	198.6	201.0	238.4	.....	249.8
B	292.6	248.3	201.4	183.2	170.9	176.7	.....	228.1

TABLE 22.—*Number of mature matings during successive 3-month periods, 1916–1919. Inbreeding and crossbreeding experiments.*

Experiment.	1916				1917				1918				1919				Year matings total.
	1–3	4–6	7–9	10–12	1–3	4–6	7–9	10–12	1–3	4–6	7–9	10–12	1–3	4–6	7–9	10–12	
2	29.0	32.3	33.0	31.0	29.0	21.7	22.3	21.0	22.7	28.7	31.0	32.7	37.3	39.0	34.0	32.7	119.4
13	36.7	33.7	34.0	31.3	24.3	16.0	16.0	14.0	12.3	13.7	17.0	18.0	19.3	23.7	25.3	27.7	90.7
32	23.3	20.0	19.0	19.0	17.0	13.0	12.0	15.0	17.0	17.0	11.7	12.3	13.7	18.0	19.0	24.0	67.8
35	29.7	24.7	23.0	22.3	20.3	18.7	16.3	20.7	22.3	21.0	20.0	22.3	22.3	29.7	31.0	35.3	94.9
39	32.3	25.3	23.7	21.0	18.7	16.7	12.0	8.7	7.7	7.3	6.3	5.0	7.3	10.0	10.7	12.3	56.3
Other	142.0	123.0	107.3	100.7	101.0	76.3	52.0	31.3	17.0	12.3	7.0	4.7	3.3	.....	.....	.....	194.5
Inbred	293.0	259.0	240.0	225.3	210.3	162.3	130.7	110.7	99.0	100.0	93.0	95.0	103.3	120.3	120.0	132.0	623.4
C0	3.0	39.0	51.3	72.3	82.3	75.3	68.3	53.7	49.0	47.7	38.3	34.7	31.0	24.3	33.7	28.7	183.2
CA	.....	.....	.....	1.3	2.7	4.0	5.0	6.0	6.7	6.0	8.0	10.0	16.7	30.7	32.0	28.7	39.4
AC	.....	.....	.....	.....	0.3	1.0	3.0	10.0	10.0	8.3	11.3	19.0	22.3	31.3	39.3	36.7	48.2
CC	.....	.....	.3	6.0	11.7	22.3	36.7	32.7	33.0	26.7	20.0	19.0	8.7	.....	.....	.....	54.3
C1	.....	.....	.3	7.0	14.0	19.0	26.0	29.0	32.3	28.0	24.0	24.7	13.3	7.3	4.3	.3	57.4
C2	.....	.....	.....	.....	.3	1.3	4.7	6.0	8.7	7.7	10.0	11.7	9.3	6.3	3.3	1.0	17.6
CL	.....	.....	.....	.....	.....	.....	.....	2.7	10.7	12.7	12.7	12.7	16.0	26.0	22.0	19.7	33.8
CG	.....	.....	.....	.....	.....	.....	.....	4.7	18.3	19.0	16.0	19.0	28.3	33.0	29.3	21.7	47.4
B	43.0	44.7	51.3	50.3	48.7	43.3	41.0	35.0	39.0	35.0	34.0	35.3	39.7	35.0	28.3	34.7	159.6

TABLE 23.—*Number of litters born during successive 3-month periods, 1916–1919. Inbreeding and crossbreeding experiments.*

Experiment.	1916				1917				1918				1919				Total.
	1–3	4–6	7–9	10–12	1–3	4–6	7–9	10–12	1–3	4–6	7–9	10–12	1–3	4–6	7–9	10–12	
2	30	26	33	27	23	25	16	22	24	22	27	30	42	36	33	25	441
13	25	26	31	22	16	9	14	15	9	10	10	15	19	23	28	21	293
32	20	16	18	15	12	11	8	16	12	11	11	8	14	18	15	18	223
35	26	20	20	23	17	15	19	18	19	15	22	18	23	26	28	32	341
39	22	19	16	18	10	12	8	9	6	7	4	2	6	6	6	12	163
Other	107	67	83	71	61	48	34	22	14	6	4	3	.....	.....	.....	.....	520
Inbred	230	174	201	176	139	120	99	102	84	71	78	76	104	109	110	108	1,981
C0	.....	17	43	56	67	63	76	44	36	29	25	22	24	24	31	31	588
CA	.....	.....	.....	.....	4	3	6	5	8	6	7	14	16	33	37	25	164
AC	.....	.....	.....	.....	.....	1	3	8	8	10	9	17	22	38	33	35	184
CC	.....	.....	1	7	12	22	47	39	33	28	21	19	9	.....	.....	.....	238
C1	.....	.....	.....	10	13	22	28	35	34	27	27	25	14	9	5	.....	249
C2	.....	.....	.....	.....	.....	2	6	7	12	6	10	11	10	6	4	1	75
CL	.....	.....	.....	.....	.....	.....	.....	1	11	7	11	12	21	31	24	20	138
CG	.....	.....	.....	.....	.....	.....	.....	9	21	20	14	21	33	36	29	27	210
B	43	36	46	45	44	40	42	33	35	30	31	34	39	33	28	29	588

TABLE 24.—*Number of young born during successive 3-month periods, 1916–1919. Inbreeding and crossbreeding experiments.*

Experiments.	1916				1917				1918				1919				Total.
	1–3	4–6	7–9	10–12	1–3	4–6	7–9	10–12	1–3	4–6	7–9	10–12	1–3	4–6	7–9	10–12	
2	59	61	78	62	47	59	36	47	49	46	56	67	100	91	82	58	998
13	59	47	90	50	37	18	34	41	24	23	21	37	58	62	79	60	740
32	44	31	41	35	24	24	17	33	24	26	28	15	26	43	39	38	488
35	69	48	58	64	41	33	43	41	41	39	53	45	54	60	71	73	833
39	50	44	41	44	26	26	13	21	13	16	12	4	16	17	12	27	382
Other	240	154	192	163	124	101	80	49	38	14	8	7	.....	.....	.....	.....	1,170
Inbred	521	385	500	418	299	261	223	232	189	164	178	175	254	273	283	256	4,611
C0	.....	32	100	118	140	137	174	97	80	63	56	57	58	64	77	81	1,334
CA	.....	.....	.....	.....	4	7	13	10	19	11	14	30	38	85	116	63	410
AC	.....	.....	.....	.....	.....	1	5	26	17	31	28	44	68	134	102	115	571
CC	.....	.....	2	16	28	51	128	90	95	68	57	48	34	.....	.....	.....	617
C1	.....	.....	.....	22	30	53	70	89	91	73	64	66	29	29	13	.....	629
C2	.....	.....	.....	.....	.....	5	11	18	30	12	22	26	26	18	12	2	182
CL	.....	.....	.....	.....	.....	.....	.....	2	27	18	25	32	50	90	83	54	381
CG	.....	.....	.....	.....	.....	.....	.....	21	49	46	43	49	105	111	82	75	581
B	115	86	139	115	105	110	106	93	87	71	79	79	123	94	82	75	1,559

TABLE 25.—*Number of young born alive during successive 3-month periods, 1916–1919. Inbreeding and crossbreeding experiments.*

Experiment.	1916				1917				1918				1919				Total.
	1–3	4–6	7–9	10–12	1–3	4–6	7–9	10–12	1–3	4–6	7–9	10–12	1–3	4–6	7–9	10–12	
2	29	49	56	42	25	39	26	43	42	34	44	59	79	71	67	48	753
13	38	35	62	36	29	12	21	28	21	11	18	30	38	56	61	42	538
32	27	20	36	27	15	19	17	25	16	19	22	15	19	41	37	31	386
35	47	36	48	45	32	20	33	35	39	19	43	37	45	44	49	63	635
39	35	32	39	28	18	18	13	19	12	13	7	4	15	16	11	25	305
Other	156	108	134	136	87	74	72	40	22	13	8	7	.....	.....	.....	.....	857
Inbred	332	280	375	314	206	182	182	190	152	109	142	152	196	228	225	209	3,474
C0	.....	22	77	71	92	115	135	86	67	42	34	47	50	54	69	76	1,037
CA	.....	.....	.....	.....	4	7	13	8	11	9	12	21	31	72	99	57	344
AC	.....	.....	.....	.....	.....	1	5	24	13	20	24	42	65	124	92	95	505
CC	.....	.....	2	13	26	41	102	78	77	58	49	46	27	.....	.....	.....	519
C1	.....	.....	.....	17	18	48	62	78	80	66	52	51	29	25	10	.....	536
C2	.....	.....	.....	.....	.....	4	11	12	26	11	18	26	24	15	8	1	156
CL	.....	.....	.....	.....	.....	.....	.....	2	16	13	19	30	43	75	73	50	321
CG	.....	.....	.....	.....	.....	.....	.....	20	32	34	28	48	79	97	73	56	467
B	93	71	121	98	79	96	90	83	65	48	64	76	112	81	70	66	1,313

TABLE 26.—*Number of young raised to weaning (33 days) during successive 3-month periods, 1916–1919. Inbreeding and crossbreeding experiments.*

Experiment.	1916				1917				1918				1919				Total
	1–3	4–6	7–9	10–12	1–3	4–6	7–9	10–12	1–3	4–6	7–9	10–12	1–3	4–6	7–9	10–12	
2	14	36	47	29	15	30	14	38	34	24	31	55	72	56	60	42	597
13	20	24	43	24	17	6	19	17	15	4	11	30	28	50	49	33	390
32	17	13	29	16	3	16	14	16	8	8	11	15	17	34	27	21	265
35	25	27	35	31	19	14	30	32	30	11	28	36	36	36	42	53	485
39	13	25	23	15	6	13	7	16	7	8	3	3	13	12	9	18	191
Other	70	81	102	78	42	60	53	31	9	7	6	5	.....	.....	.....	.....	544
Inbred	159	206	279	193	102	139	137	150	103	62	90	144	166	188	187	167	2,472
C0	.....	16	62	54	63	103	110	79	55	33	31	43	43	50	66	63	871
CA	.....	.....	.....	.....	4	7	11	5	10	6	11	20	27	68	91	55	315
AC	.....	.....	.....	.....	.....	1	5	17	10	9	22	39	60	104	85	83	435
CC	.....	.....	1	8	12	41	74	74	59	44	37	45	18	.....	.....	.....	413
C1	.....	.....	.....	8	12	40	55	70	59	41	39	46	29	20	9	.....	428
C2	.....	.....	.....	.....	.....	2	11	9	13	9	15	26	24	10	5	1	125
CL	.....	.....	.....	.....	.....	.....	.....	2	10	11	16	27	35	69	67	44	281
CG	.....	.....	.....	.....	.....	.....	.....	18	19	28	22	48	61	80	64	47	387
B	74	60	97	75	52	80	75	72	57	38	44	74	85	66	61	61	1,071

TABLE 27.—*Indices and averages, showing the record of the total inbred stock in various characteristics during successive 3-month periods, 1916–1919.*

Character.	1916				1917				1918				1919			
	1–3	4–6	7–9	10–12	1–3	4–6	7–9	10–12	1–3	4–6	7–9	10–12	1–3	4–6	7–9	10–12
Per cent born alive	65.6	74.5	80.4	78.3	67.1	69.9	84.1	83.8	82.1	69.9	80.7	87.3	81.9	84.0	86.0	84.0
Per cent raised of born alive	47.3	74.6	78.8	61.8	47.6	73.0	76.5	79.3	68.6	57.0	66.0	94.7	86.2	87.3	87.6	80.0
Per cent raised	32.4	56.0	63.0	49.3	32.8	53.8	63.9	66.8	57.0	40.4	53.0	82.7	70.5	73.4	75.8	67.9
Birth weight (total)	69.6	71.0	68.5	71.9	64.5	65.0	66.3	75.3	69.8	63.8	66.0	81.9	83.1	83.1	79.1	76.6
Birth weight (raised)	76.3	77.9	73.6	77.6	72.3	72.4	70.9	78.0	73.3	71.1	73.0	85.1	85.2	85.7	81.9	78.3
Gain	3.18	3.32	3.04	3.15	3.19	3.07	3.70	4.11	3.55	2.72	3.22	5.20	4.43	4.43	3.89	3.73
Weight, 33 days	181.3	187.4	174.0	181.4	177.6	173.8	192.9	213.6	190.6	160.8	179.1	256.8	231.5	232.0	210.3	201.3
Size of litter	2.27	2.21	2.49	2.38	2.15	2.18	2.25	2.27	2.25	2.31	2.28	2.30	2.44	2.50	2.57	2.37
Litters per year	3.14	2.69	3.35	3.13	2.64	2.96	3.03	3.68	3.39	2.84	3.36	3.19	4.03	3.62	3.67	3.27
Young per year	7.12	5.94	8.33	7.42	5.68	6.43	6.82	8.38	7.62	6.56	7.67	7.35	9.84	9.07	9.43	7.76
Young raised per year	2.17	3.18	4.65	3.43	1.94	3.43	4.19	5.42	4.16	2.48	3.87	6.06	6.43	6.25	6.23	5.06
Sex ratio	120.3	88.3	93.2	104.0	105.0	111.0	109.9	90.0	86.3	118.1	116.5	98.8	130.6	110.2	102.2	101.6

TABLE 28.—*Indices and averages showing the estimated record of the total inbred stock during the period in which each experiment was in progress.*

Experiment.	Per cent born alive.	Per cent raised of those born alive.	Per cent raised.	Birth weight, total.	Birth weight of those raised.	Gain per day.	Weight at 33 days.	Size of litter.	Litters per year.	Young per year.	Young raised per year.
				Grams.	*Grams.*	*Grams.*	*Grams.*				
2	79.3	76.4	60.6	73.5	78.8	3.81	204.6	2.34	3.27	7.69	4.42
13	79.5	75.4	60.7	73.6	78.9	3.79	203.9	2.35	3.23	7.57	4.21
32	78.6	74.2	58.4	72.6	78.3	3.72	201.0	2.34	3.24	7.59	4.24
35	79.1	73.9	59.2	72.9	78.6	3.74	201.4	2.34	3.27	7.68	4.40
39	76.6	70.8	54.4	71.2	77.3	3.54	194.2	2.32	3.17	7.34	3.85
Other	74.3	65.4	49.7	69.0	75.0	3.28	183.2	2.29	3.03	6.93	3.30
Inbred	77.7	72.1	56.3	71.8	77.6	3.64	197.8	2.33	3.18	7.40	3.96
C0	79.0	74.1	58.8	71.0	76.4	3.64	195.6	2.31	3.18	7.35	4.09
CA	83.6	83.0	70.1	77.9	81.0	4.02	213.8	2.41	3.48	8.42	5.42
AC	83.3	83.2	69.4	78.2	81.7	4.12	217.7	2.41	3.49	8.45	5.51
CC	79.9	72.6	58.9	70.0	75.2	3.71	197.6	2.27	3.22	7.31	4.17
C1	79.8	73.5	59.6	71.2	76.3	3.77	200.8	2.29	3.25	7.46	4.31
C2	82.3	78.9	65.3	74.8	79.3	4.10	214.5	2.33	3.40	7.96	4.94
CL	83.4	83.3	69.5	78.2	81.7	4.10	217.0	2.42	3.47	8.38	5.32
CG	82.6	81.9	67.5	77.4	81.3	4.10	216.6	2.40	3.48	8.39	5.32
B	78.4	73.3	58.2	72.1	77.3	3.66	198.0	2.32	3.22	7.51	4.19

TABLE 29.—*Indices and averages showing the record of each experiment during the portion of the 4 years, 1916–1919, in which it was in progress.*

Experiment.	Per cent born alive.	Per cent raised of those born alive.	Per cent raised.	Birth weight, total.	Birth weight of those raised.	Gain per day.	Weight at 33 days.	Size of Litter.	Litters per year.	Young per year.	Young raised per year.
				Grams.	*Grams.*	*Grams.*	*Grams.*				
2	75.6	79.4	60.3	66.6	72.7	3.10	175.1	2.26	3.70	8.37	5.00
13	78.2	74.0	58.0	76.1	83.7	4.29	225.2	2.53	3.23	8.16	4.30
32	80.8	68.2	55.1	74.3	78.9	3.73	201.9	2.19	3.29	7.20	3.91
35	79.8	78.0	62.4	77.1	81.6	4.18	219.6	2.44	3.59	8.78	5.11
39	81.0	65.4	54.0	67.9	73.3	3.50	189.1	2.34	2.90	6.79	3.39
Other	75.4	63.6	48.1	70.9	76.2	3.30	185.0	2.25	2.67	6.01	2.80
Inbred	77.7	72.1	56.3	71.8	77.6	3.64	197.8	2.33	3.18	7.40	3.96
C0	79.5	84.8	67.8	72.2	78.3	4.12	214.2	2.27	3.21	7.28	4.48
CA	85.8	91.7	78.8	80.7	83.9	4.49	232.1	2.50	4.16	10.41	7.99
AC	89.5	91.4	81.7	85.1	88.3	4.61	240.5	3.10	3.82	11.85	9.02
CC	86.3	84.5	73.1	79.0	82.1	4.49	230.3	2.59	4.38	11.36	7.61
C1	88.2	82.5	73.0	78.8	81.7	4.37	225.8	2.53	4.34	10.96	7.46
C2	85.6	85.5	73.4	79.8	82.9	4.62	235.5	2.43	4.26	10.34	7.10
CL	91.3	86.8	79.2	84.7	85.4	4.99	250.2	2.76	4.08	11.27	8.31
CG	86.9	86.4	75.3	83.6	88.1	4.90	249.8	2.77	4.43	12.26	8.16
B	86.8	83.8	72.8	79.9	84.6	4.35	228.1	2.65	3.68	9.77	6.71

TABLE 30.—*Differences between the records of each experiment and those of the total inbred stock, raised simultaneously.*

[Obtained by subtracting the entries in Table 28 from those in Table 29. 1916–1919.]

Experiment.	Per cent born alive.	Per cent raised of those born alive.	Per cent raised.	Birth weight, total.	Birth weight of those raised.	Gain per day.	Weight at 33 days.	Size of litter.	Litters per year.	Young per year.	Young raised per year.
				Grams.	*Grams.*	*Grams.*	*Grams.*				
2	−3.7	+3.0	−0.3	−6.9	−6.1	−0.71	−29.5	−0.08	+0.43	+0.68	+0.58
13	−1.3	−1.4	−2.7	+2.5	+4.8	+.50	+21.3	+.18	.00	+.59	+.09
32	+2.2	−6.0	−2.3	+1.7	+0.6	+.01	+0.9	−.15	+.05	−.39	−.33
35	+0.7	+4.1	+3.2	+4.2	+3.6	+.44	+18.2	+.10	+.32	+1.10	+.71
39	+4.4	−5.4	−1.4	−3.3	−4.0	−.04	−5.1	+.02	−.27	−.55	−.46
Other	+1.1	−1.8	−1.6	+1.9	+1.2	+.02	+1.8	−.04	−.36	−.92	−.50
C0	+1.5	+10.7	+9.0	+1.2	+1.9	+.48	+17.6	−.04	+.03	−.07	+.39
CA	+2.2	+8.7	+8.7	+2.8	+2.9	+.47	+18.3	+.09	+.68	+1.99	+2.57
AC	+6.2	+8.2	+12.3	+6.9	+6.6	+.49	+22.8	+.69	+.33	+3.40	+3.51
CC	+6.4	+11.9	+14.2	+9.0	+6.9	+.78	+32.7	+.32	+1.16	+4.05	+3.44
C1	+8.4	+9.0	+13.4	+7.6	+5.4	+.60	+25.0	+.24	+1.09	+3.50	+3.15
C2	+3.3	+6.6	+8.1	+5.0	+3.6	+.52	+21.0	+.10	+.86	+2.38	+2.16
CL	+7.9	+3.5	+9.7	+6.5	+3.7	+.89	+33.2	+.34	+.61	+2.89	+2.99
CG	+4.3	+4.5	+7.8	+6.2	+6.8	+.80	+33.2	+.37	+.95	+3.87	+2.84
B	+8.4	+10.5	+14.6	+7.8	+7.3	+.69	+30.1	+.33	+.46	+2.26	+2.52

TABLE 31.—*Estimated probable errors of the indices and averages of Table 29.*

Experiment.	Per cent born alive.	Per cent raised of those born alive.	Per cent raised.	Birth weight, total.	Birth weight of those raised.	Gain per day.	Weight at 33 days.	Size of litter.	Litters per year.	Young per year.	Young raised per year.
				Grams.	*Grams.*	*Grams.*	*Grams.*				
2	1.2	1.2	1.3	0.40	0.47	0.044	1.71	0.028	0.060	0.190	0.154
13	1.3	1.6	1.6	.48	.59	.056	2.16	.042	.085	.216	.174
32	1.5	2.0	1.9	.57	.70	.066	2.56	.042	.096	.239	.199
35	1.2	1.4	1.4	.44	.53	.050	1.91	.037	.071	.217	.173
39	1.7	2.3	2.2	.65	.84	.079	3.06	.055	.123	.258	.217
Other	1.1	1.4	1.3	.37	.49	.047	1.80	.028	.072	.134	.115
Inbred	.5	.6	.6	.19	.23	.022	.85	.015	.033	.080	.066
C0	1.0	.9	1.1	.35	.39	.037	1.43	.027	.060	.146	.123
CA	1.5	1.3	1.8	.64	.67	.064	2.45	.057	.079	.359	.284
AC	1.2	1.2	1.5	.59	.60	.057	2.19	.063	.088	.343	.261
CC	1.2	1.4	1.6	.52	.58	.054	2.09	.047	.058	317	.240
C1	1.1	1.4	1.6	.52	.57	.054	2.07	.047	.058	.303	.232
C2	2.2	2.4	2.8	.95	1.04	.099	3.80	.078	.111	.537	.418
CL	1.2	1.7	1.8	.66	.73	.069	2.67	.070	.091	.401	.308
CG	1.3	1.4	1.6	.56	.61	.058	2.23	.056	.059	.351	.259
B	.8	.9	1.0	.33	.36	.034	1.32	.030	.052	.174	.137

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